AFFINITIES BETWEEN THE WEST PALAEARCTIC AND ETHIOPIAN BUTTERFLY FAUNAS

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With ten figures

ABSTRACT

A survey is given of the species and genera common to the West Palaearctic and Ethiopian Regions. The possibilities of a faunal exchange in the past, especially during the Pleistocene, are analysed and related to the present distribution of West Palaearctic species in the Ethiopian Region and vice versa. It is demonstrated that faunal exchange across the Saharo-Arabian desert zone was not infrequently possible, but most invading species died out subsequently. Palaearctic species in the Ethiopian Region had a better chance to survive than Ethiopian species in the Palaearctic Region. Although the bare condition of the desert zone at present keeps the Palaearctic and Ethiopian Regions apart, it is concluded that the main factor inhibiting large-scale faunal exchange during the Pleistocene has been the repeated change of climate.

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1. Introduction

General

This study is a zoogeographic one. It tries to describe the affinities between the butterfly faunas of the West Palaearctic and Ethiopian Regions and to explain these affinities with the aid of possible past distributions. As it deals with distributions, the ranges of the species have to be known and in this respect the butterflies form an attractive group, because possibly no insect group is better known.

This study also deals with history and, therefore, is concerned with evolution. In this respect, butterflies are probably scarcely better known than any other group of insects, as by far the greater part of the extensive literature on butterflies is faunistic (i.e., a description of the composition of species of a certain area) or a detailed analysis of the wealth of forms. At least the lower classification of the butterflies is still largely typological and evolutionary studies are almost absent. This is felt as a hindrance for the present paper, as an evolutionary study may reveal much of the probable geographic history (cf. De Jong, 1974). Nevertheless, there is no reason to suppose that an evolutionary study of the butterflies will necessitate many alterations in the classification and for the present paper I assume that the generally accepted genera are monophyletic. Further, if a genus has many representatives in region A, one of which occurs (possibly in another form) in region B, where it is the sole representative of the genus, it is concluded that this particular species invaded B from A. In some cases, viz. migrants, there is direct evidence of such invasions. In other cases, evidence or at least support should be looked for in an evolutionary study and in this way the present paper may serve to indicate some of the many gaps in our knowledge.

I have attempted to give the total number of species known for each genus, but have often failed to find agreement in literature. This is due partly to (sometimes excessive) splitting of genera and species, partly to the fact that, usually, regional faunas instead of whole genera have been studied and I cannot help thinking that various degrees of "intuition" have played a part. It is, for instance, difficult to estimate the number of species in the genus *Lycaena* (the Coppers). Kostrowicki (1969) lists 30 species in the Palaearctic Region, but generally this genus is divided into four genera (*Heodes, Lycaena, Thersamonia* and *Palaeochrysophanus*) in the West Palaearctic. For Central Europe, Forster & Wohlfahrt (1955) place the species *helle* and *phlaeas* in *Lycaena* s.s. and *dispar* in *Thersamonia*, while Higgins & Riley (1970) consider *dispar* congeneric with *phlaeas*. If there is so much disagreement in the best known part of the world, how about the Asiatic species, for which Verity (1943) introduced two more genera. In such cases it seems most practical to record the number of species in the collective genus, in the above case

Lycaena s.l. In the text it is specified how the total number of species in a genus has been arrived at. It is not of crucial importance for the present study. So far as the genera can be considered monophyletic, large genera may be preferable for the present kind of study, as they may give a good impression of the relative development of a group of species in various regions, e.g. the very strong development of the Coppers (*Lycaena* s.l.) in the Holarctic Region as opposed to the very poor representation outside this area. On the other side, however, it is also indicative to observe that the Coppers in the Holarctic Region can be divided into six genera, while only one of these genera, with a single group of species, occurs in the Ethiopian Region. An advantage of the use of many small genera is that it is easier for a non-specialist to trace closely related species (if the small genera are considered monophyletic, what can only be assumed as they are usually based typologically).

The affinities between the West Palaearctic and Ethiopian butterfly faunas have been studied up to the generic level, i.e. only common genera have been considered. The affinities based on related instead of common genera have been regarded too remote to be studied successfully on the basis of the present-day knowledge of both the phylogeny of the butterflies and the geographic and climatic changes in the more remote past. Another limitation to the present paper is the area studied. As is known many Oriental genera penetrate the Palaearctic Region in East Asia. Some of these genera (e.g. *Graphium, Appias, Mycalesis, Deudorix*) also occur in the Ethiopian Region and in such cases it is probable that the affinities between the Palaearctic and Ethiopian Regions are indirect, via the Oriental Region. To exclude such cases, only the butterfly genera occurring in the West Palaearctic Region, west of about 50° E Long. (thus including Europe and the Middle East), have been considered.

The Palaearctic-Ethiopian boundary

There is some disagreement about the boundary between the Palaearctic and Ethiopian Regions. Darlington (1957), for instance, delimited the Ethiopian Region as the whole of Africa except the parts of Morocco and Algeria north of the Atlas Mountains, while De Lattin (1967) sets the boundary along the southern edge of the Sahara. There is no reason to enter here into a discussion on the use of distinguishing zoogeographic regions, but as descriptive, geographic terms they have at least practical value, provided they are clearly defined. The obstacle in defining the boundary between the Palaearctic and Ethiopian Regions is the position of the Sahara. Although often the peculiar character of its fauna is recognized, the Sahara is still usually considered a transition zone. Geographically the Sahara is, indeed, the transition between the tropical parts of Africa and the warm-temperate parts of the northern part of the Old World. Ecologically, however, speaking in terms of major habitats, the Sahara is a life zone, a biome, comparable in this respect to, e.g., the taiga or the sea. I never saw the taiga considered the transition between the deciduous forests to the south and the subarctic birch forest to the north. And there is apparently little meaning in calling the sea the transition zone between two land masses or in regarding Africa the

transition zone between the Atlantic and Indian Oceans, just because it lies in between.

The zoogeographic distinction of the Palaearctic and Ethiopian Regions is based on a different faunal composition. This difference can, at least partly, be explained as the result of a separated faunal development, i.e. there has been a barrier preventing free faunal exchange. Evidently the main barrier has been and is the Sahara.

These considerations lead to the assumption that the boundary between the Palaearctic and Ethiopian Regions does not run north or south of or straight across the Sahara, but is the Sahara itself. Studying the affinities between the butterfly faunas of the Palaearctic and Ethiopian Regions is studying the function of the Sahara as a barrier, at present and in the past. As a consequence, only those genera and species are considered common to both regions, which occur north as well as south of the Sahara.

The area studied has been extended to the east to cover the Arabian peninsula, extending the barrier to the Saharo-Arabian desert zone and regarding Yemen the north-eastern outpost of the Ethiopian Region.

2. RANGE, ECOLOGY AND RELATIONSHIP OF GENERA AND SPECIES OF BUTTERFLIES COMMON TO THE WEST PALAEARCTIC AND ETHIOPIAN REGIONS

Papilio. A cosmopolitan genus with a large development in the tropics, but with only three species in the West Palaearctic, viz. *machaon* L., *hospiton* Géné, and *alexanor* Esper. The Ethiopian fauna comprises about 50 species. Over the whole more than 200 species are known. The West Palaearctic species are placed by Munroe (1960) in the *machaon* group, which ranges throughout the Holarctic Region and into Central America. Together with the East Palaearctic *xuthus* L., they are thought to be closely related to the *demoleus* group, which occurs in the Ethiopian and Oriental Regions and extends eastward to Papua.

Pieris. Much disagreement exists in the delimitation of the genera *Pieris* and *Pontia.* Part of the disagreement is shown in Table 1. The number of species allocated to *Pieris* varies from about 18 to about 26, see e.g. Talbot (1932a) and Bernardi (1947). Of these six to nine are confined to the New World. In the Old World the genus is almost strictly Palaearctic, but some species extend far into the Oriental Region (*canidia* Sparrman, *melete* Ménétriés) or occur near the edge of the Palaearctic (*naganum* Moore). One species, *rapae* L., has been imported as far as New Zealand (Laidlaw, 1970). Apparently, an Oriental development of the genus is absent. In the Ethiopian Region there is a single, endemic species, viz. *brassicoides* Guérin, which is restricted to the montane grasslands of Ethiopia and N. Tanzania (Carcasson, 1964). The latter population was distinguished as ssp. *meridionalis* Joicey et Talbot. According to Lagnel (1966) *brassicoides* can be considered to form a superspecies together with *brassicae* L. (Canary Islands, N. Africa and W. Europe to Yunnan) and *deota* De Nicéville (Issyk-Kul to Ladak). The common European *brassicae* (Large White) can be found everywhere in flowery places from lowlands up to 2000 m (Fig. 3).

Pontia. Part of the disagreement on the delimitation of this genus is shown in

Table 1. We are here mainly interested in the first four species on which there is no disagreement with regard to the genus they belong to and which as a group occur in the Ethiopian and Palaearctic Regions. But to place their evolution in a wider perspective, also the other, probably closely related species listed in Table 1

Table 1. Allocation of species to *Pontia* and related genera by various authors

	Talbot (1932a)	Verity (1947)	Bernardi (1947)	Dos Passos (1964)	Higgins & Riley (1970)
daplidice	*Pontia*	*Pontia*	*Pontia*	—	*Pontia*
glauconome	*Pontia*	*Pontia*	*Pontia*	—	—
distorta	*Pontia*	*Pontia*	—	—	—
helice	*Pontia*	*Pontia*	—	—	—
chloridice	*Pontieuchloia*	*Pontieuchloia*	*Pieris*	—	*Pontia*
beckeri	*Pontieuchloia*	*Pontieuchloia*	*Pieris*	*Pieris*	*Pontia*
protodice	*Pontieuchloia*	*Synchloe*	*Pieris*	*Pieris*	—
sisymbrii	*Pontieuchloia*	*Synchloe*	*Pieris*	*Pieris*	—
callidice	*Synchloe*	*Synchloe*	*Pieris*	—	*Pontia*
dubernardi	*Synchloe*	*Synchloe*	*Pieris*	—	—
davidis	*Synchloe*	*Synchloe*	*Pieris*	—	—
nigricans	*Synchloe*	*Synchloe*	*Pieris*	—	—

have to be considered and without choosing for one of the classifications mentioned the following observations may be important for the present study:

a. All species of Table 1 are confined to some part of the Holarctic Region, except the first four species, two of which are Ethiopian, while the other two occur in both the Ethiopian and Palaearctic Regions.

b. *Pontieuchloia* is considered intermediate between *Pontia* and the almost exclusively Holarctic *Euchloe* (Verity, 1947).

c. According to Verity (1947) the last three species of Table 1 are intermediate between *Synchloe* and the Palaearctic genus *Aporia*.

All these observations point to an almost entirely Holarctic group of species with a slight development in the Ethiopian Region. As related genera occur in the Palaearctic and not in the Ethiopian Region, the Palaearctic origin of the Ethiopian members seems obvious.

The ranges, etc., of the first four species of Table 1 are as follows:

daplidice L. — From France to Japan (Higgins & Riley, 1970); Canary Islands (Van Regteren Altena, 1949); N. Africa south to Tibesti (Bernardi, 1962). In all these regions there is little geographic variation (though various subspecies have been described), possibly due to the fact that the species, at least in Europe, is strongly migratory. A separate subspecies (*aethiops* Joannis et Verity) is recorded from Ethiopia, Somalia and Yemen (Gabriel, 1954). *P. daplidice* prefers rough grounds and flowery meadows.

glauconome Klug. — An eremic species occurring from Mauretania to Ethiopia, Kenya, Somalia and Sinai and through Arabia and Mesopotamia to NW. India. The African and Arabian populations are thought to be subspecifically distinct (ssp. *glauconome* Klug) from the more eastern populations (ssp. *iranica* Bien.).

distorta Butler. — Restricted to Somalia and Kenya (Aurivillius, 1910—25). Probably also a more or less eremian species.

helice L. — A common species throughout S. Africa (Swanepoel, 1953), north to

S. Botswana and S. Rhodesia (Van Son, 1949). Further, in the montane grasslands of E. Africa (Kivu, Tanzania, Uganda, Kenya) as a separate subspecies (*johnstoni* Crowley) (Fig. 5).

Euchloe. This genus is divided by Bernardi (1945) and Verity (1947) into two subgenera, viz. *Elphinstonia* and *Euchloe*. Higgins & Riley (1970) consider *Elphinstonia* a separate genus, but their allocation of species to *Euchloe* and *Elphinstonia* is different from Bernardi's and Verity's. This difference of opinion is unimportant for the present study and we will distinguish a single genus, like Bernardi did, but without bothering about subgenera.

The genus *Euchloe* comprises ten species. Three species are confined to N. America; the remainder are Palaearctic, but two species also occur in the Ethiopian Region, viz.:

belemia Esper. — SW. Europe, Canary Islands, N. Africa (also Tibesti) to Iran and Baluchistan (Higgins & Riley, 1970). In the Ethiopian Region it is known from Ethiopia and Somalia (Talbot, 1932b; Carpenter, 1935). The Ethiopian populations are distinguished as ssp. *abyssinica* Riley. This species prefers rough, flowery places, usually at low levels. It is a strong flyer; in S. Spain I had no difficulty in distinguishing this species among other spring species like *Pontia daplidice, Euchloe ausonia* and *Pieris rapae*, by its flight only.

fallomi Allard. — More eremic than *belemia*, ranging far into desert oases and occurring throughout N. Africa, including Tibesti, Fezzan, Tripoli, and Egypt, but in the north-west mainly south of the Atlas Mountains (Higgins & Riley, 1970). In the Ethiopian Region it has been found in Somalia. According to Talbot (1932a) the Somalia population represents the same subspecies as which flies in S. Algeria (*obsolescens* Rothschild). Gabriel (1954) recorded this species from SW. Arabia, with the comment that this population may represent a separate subspecies.

Colotis. An Indo-African genus, with 40 Ethiopian species (Carcasson, 1964) and seven species in India and Ceylon (Wynter-Blyth, 1957). Almost all species occur in open and usually dry country and many species live partly or exclusively in semidesert environments. There are no endemic Palaearctic species, but some species penetrate into the southern parts of the Palaearctic. They are:

evagore Klug. — Throughout the Ethiopian Region (Williams, 1969) and in Yemen (Gabriel, 1954); as a separate subspecies, *nouna* Lucas, in Morocco, Algeria, Tunis and S. Spain (Higgins & Riley, 1970) (Fig. 7).

fausta Oliv. — India to Egypt and SW. Arabia; north to Israel and Jordania (Hemming, 1932) and, as a migrant, in Lebanon and sometimes Turkey (Larsen, 1974). Although it is a common species in Lebanon, *fausta* appears unable to hibernate there.

calais Cramer. — Through most of the Ethiopian Region outside forest areas. In the Oriental Region in India and Ceylon. It occurs in Yemen (Gabriel, 1954) and seems to be resident as far north as Ennedi (Bernardi, 1964) and the Aïr Mountains (Rothschild, 1921) in the Sahara, and the Jordan Valley (Larsen, 1974). Talbot (1934) considered the E. Mediterranean form indistinct from the Indian one, but according to Gabriel (1954) and Larsen (1974) the African form flies there.

phisadia Godart. — NW. India, Arabia to Nubia, Ethiopia, Somalia, Kenya, Senegal (Talbot, 1934) and Rio de Oro (Bernardi, 1966). Also known from Ennedi, Tibesti, Ahaggar and Aïr (cf. Table 5) in the Sahara. Talbot mentioned Madagascar but this seems an improbable locality. In Israel and Jordania it flies as ssp. *palaestinensis* Staudinger (Hemming, 1932; Talbot, 1934).

chrysonome Klug. — According to Talbot (1934) from S. Israel and Jordania through Arabia, Nubia and Somalia to Tanzania and N. Rhodesia; further in N. Nigeria and Rio de Oro (Bernardi, 1966) and mentioned from Ennedi, Tibesti, Ahaggar and Aïr in the Sahara (cf. Table 5).

Anaphaeis. A palaeotropical genus with two species in the Indo-Australian Region and seven in Africa and Madagascar. There are no endemic Palaearctic species. The species *aurota* Fabr. occurs throughout Africa south of the Sahara, in a variety of habitats, from forest edges to semidesert bush (Williams, 1969). Further north it occurs in Sudan, Egypt and Arabia (Gabriel, 1954) and, as a migrant, in Lebanon (Larsen, 1974) and Jordania (Hemming, 1932). It extends further east through India to Ceylon (Wynter-Blyth, 1957).

Catopsilia. This genus has a peculiar distribution. According to Talbot (1932a) there are three species in Madagascar (and Mauritius) and five in the Indo-Australian Region, while one species, viz. *florella* Fabr., flies throughout the Ethiopian Region and extends via Egypt and Arabia to India, China and Hainan. Only since 1966 it is known from the Canary Islands where it has become established probably as a result of migration (Manley & Allcard, 1970). It has been found as a migrant in Lebanon (Larsen, 1974) and Iraq (Wiltshire, 1957).

Colias. This genus reaches its greatest development in the Holarctic Region where about 50 species occur (36 in the Palaearctic). In the Neotropical Region 12 species are known. Although 14 species have been found in India, they cannot be regarded Oriental residents, as they are confined to the higher altitudes of the Himalayas, with the exception of *erate* Esper (Wynter-Blyth, 1957). The literature is somewhat confused about the identity of the Indian *erate*, but that is not important here. The Indian *erate* occurs in NW. India (Chitral to Kumaon) and in the S. Indian mountains.

In the Ethiopian Region two species of *Colias* are known, viz.:

erate Esper. — Palaearctic, from E. Europe to Japan and Formosa (Higgins & Riley, 1970) and in India (see above). Further in Ethiopia, Somalia, Sudan, Egypt and SW. Arabia (Gabriel, 1954) (ssp. *marnoana* Rogenhofer).

electo L. — According to Williams (1969) distributed over the greater part of Africa south of the Sahara, in grasslands, along forest edges, etc., but I have not found data on its occurrence in W. Africa. Outside Africa, it has been found in Yemen en Saudi-Arabia (Gabriel, 1954). Aurivillius (1910—25) and Van Son (1949) regarded *electo* conspecific with *crocea* Geoffroy, but various authors (e.g. Lempke, 1944 (1946); Jarvis, 1953) concluded on typological grounds that *crocea* and *electo* are specifically distinct. *C. crocea* is a well-known migrant in Europe which occurs from the Azores, Madeira and Canary Islands through N. Africa and S. and C. Europe to Iran (Higgins & Riley, 1970). In N. Africa *crocea* goes as far south as Tibesti (Bernardi, 1962).

Jarvis (1953) suggested that the E. African form of *electo, pseudohecate* Berger, could be a species separate of *electo*, but we will not busy ourselves with such speculations.

Note. I have no special knowledge of the genus *Colias*, but it appears to me that the Ethiopian species can be considered to belong to two species groups, viz.:

a. the *hyale* group, comprising *hyale* L. (C. Europe to Altai; strongly migratory), *australis* Verity (S. and C. Europe to S. Russia and Turkey; possibly migratory) and *erate* Esper (E. Europe to Japan and Formosa; south to Ethiopia, Somalia, S. India).

b. the *crocea* group, comprising *crocea* Geoffroy (W. Palaearctic to Iran; strongly migratory), *fieldii* Ménétriés (N. India to N. Burma, at higher altitudes) and *electo* (Ethiopian Region to Arabia) (cf. Lempke, 1944 (1946); Jarvis, 1953).

Classified in this way it is striking that these groups are the only groups of *Colias* species in the Old World represented outside the Palaearctic Region, and that both possess at least one species that is strongly migratory. It seems inevitable to consider the Ethiopian species Palaearctic invaders.

Danaus. A pantropical genus with about 60 species. A few species occur in the Nearctic Region, a few others penetrate the Palaearctic Region in the east and two have been found in the W. Palaearctic, mainly as migrants. They are:

plexippus L. — An American species that since 1880 is resident in the Canary Islands. It also occurs in the Azores. Rare vagrants reach Portugal, Spain, France, Ireland and England (Higgins & Riley, 1970). This species has extended its range from America particularly in western direction, largely aided by man, and it now occurs in Hawaii, New Zealand, Australia, Papua, Indonesia, Formosa and the Andaman Islands (Klots, 1951; Higgins & Riley, 1970). It is absent from Africa and continental Asia.

chrysippus L. — A very common species throughout the Ethiopian Region, in open and bush country, gardens, woodlands, margins of forests (Williams, 1969). Resident in the Canary Islands. North to Lebanon and thence eastward throughout tropical Asia to Australia; vagrants occasionally found in Morocco, S. Italy and Greece (Larsen, 1974). In Africa it occurs in two subspecies:

a. ssp. *alcippus* Cramer. — W. Africa south of the Sahara, north to S. Morocco and also found in Aïr, Tibesti and Ennedi in the Sahara.

b. ssp. *chrysippus* L. — Whole of Africa, except the west; eastern Mediterranean and thence eastward. According to Bernardi (1962) this form also occurs in the Canary Islands, but Manley & Allcard (1970) list the form of that area as a distinct, endemic subspecies (*kanariensis* Fruhst.).

Libythea. A peculiar, cosmopolitan genus with about ten species (the two New World species are classified by Dos Passos, 1964, in a separate genus). Pagenstecher (1901) distinguished two subgenera in the Old World, viz. *Libythea* with six species, in Europe, Asia and Australia; and *Dichora* with three species, in the Ethiopian Region (one confined to Madagascar and Mauritius). Williams (1969) considered one of the Ethiopian species of Pagenstecher (*laius* Trimen) a subspecies of the Ethiopian *labdaca* Westwood, and according to Corbet & Pendlebury (1956) *labdaca* is the Ethiopian representative of the Oriental *narina*

Godart, so that the distinction of two subgenera is insignificant.

In the West Palaearctic only *celtis* Laich. occurs. Its range extends from S. Europe and N. Africa to Japan and Formosa. From the above it seems improbable that there is a direct relationship between the West Palaearctic and Ethiopian species.

Charaxes. A palaeotropical genus with 86 species in Africa south of the Sahara (Carcasson, 1964) and more than 20 in the Indo-Australian Region. There is only a single species occurring in the Palaearctic Region and this species also flies throughout the Ethiopian Region, viz. *jasius* L. (Fig. 9). It was apparently by mistake that Carcasson called *Charaxes* a Palaearctic genus.

The distribution of *jasius* in the Palaearctic is confined to the coastal areas around the Mediterranean. South of the Sahara, *jasius* occurs in two distinct geographic forms all over the continent, in savanna country, woodlands and bush.

Neptis. Apart from a large development in the Ethiopian Region (47 species; Carcasson, 1964), there are many species confined to the Indo-Australian area (31) and to the Palaearctic (18), while 20 species occur in both the Palaearctic and Oriental Regions (Eliot, 1969). Most Palaearctic species are confined to East Asia, often to the contact zone with the Oriental Region; only two species occur as far west as Europe:

sappho Pallas. — A woodland species, distributed from C. Europe (Salzburg) to the Amur region, Japan, Formosa and S. Vietnam, in a number of subspecies.

rivularis Scopoli. — Also a woodland species, from the Southern Alps (Piedmont) to Kamchatka, Kurile Is., Japan, Formosa and Szechwan, in a number of subspecies.

There is no apparent reason to suppose a close relationship between the two mentioned species and the Ethiopian members of the genus. On the contrary, the European species appear Asiatic invaders in Europe, judged from their present distribution.

Hypolimnas. A palaeotropical genus with a twenty odd species. Two species occur in Africa as well as in the Indo-Australian area and one of these, *misippus* L., is rarely found as a migrant in Lebanon, probably coming from Egypt, where it is common (Larsen, 1974). This species has a very extensive range. It occurs from Madagascar and Africa (where it is common everywhere in open country, bush, etc.; Williams, 1969) to India, SE. Asia, New Guinea, Solomons Islands, and Australia. It was supposedly introduced into the Antilles from Africa in slave ships some centuries ago and has been found not only in the West Indies, but also north into the USA and in northern S. America (Common & Waterhouse, 1972).

Vanessa. This genus was recently dealt with by Field (1971), who thought it necessary to split *Vanessa* in three genera, viz. *Vanessa, Bassaris* and *Cynthia*. In my opinion this splitting is somewhat superfluous, as for the reflection of the affinities within the genus the distinction of species groups or subgenera would have done and nomenclatorial troubles would have been avoided. I deal with the genera of Field here as subdivisions of the genus *Vanessa* s.l. This genus is, with 16 species, distributed all over the world. Four species have been found in the West

Palaearctic and one of these is the sole representative of the genus in the Ethiopian Region. They are:

atalanta L. — According to Field (1971), a Holarctic species that is introduced in Hawaii, but Higgins & Riley (1970) thought its Palaearctic range not to extend eastward beyond Iran. No subspeciation within the Palaearctic. It is a well-known migrant in Europe and in the northern part of its range it reintroduces itself each year by migrations from the south.

Together with the following and three other species, *atalanta* belongs to *Vanessa* s.s., which is distributed in the Holarctic and Oriental Regions.

indica Herbst. — This species shows a peculiar distribution: it is widely distributed in India, China, Korea and Japan, and quite separated from this range it occurs in Madeira and the Canary Islands (distinguished as ssp. *vulcanica* Godart).

cardui L. — The most cosmopolitan butterfly, found everywhere, except in Australia and New Zealand (where it is replaced by *kershawi* M'Coy) and in arctic and antarctic regions. It is rare in S. America south of Venezuela. This species is strongly migratory and this may be the reason why there is no geographic variation, though subspecies have been described (see Field, 1971). In much of Europe, *cardui* cannot hibernate, but can produce a summer generation. It is the only *Vanessa* species in Africa. With the Australian *kershawi* and seven New World species *cardui* forms what Field called the genus *Cynthia*.

virginiensis Drury. — One of the New World species of Field's *Cynthia*, occurring from Canada to Colombia and Venezuela and possibly much further south (Field, 1971). Field recorded this species to have become established by migration in Hawaii, the Azores, Madeira and the Canary Islands, but Higgins & Riley (1970) and Manley & Allcard (1970) only mentioned the Canary Islands, as far as the Palaearctic is concerned. Since 1948 many specimens have been found in Portugal and some also in Spain, as far as the Pyrenees (Gomez Bustillo & Rubio, 1974). No subspecies are known.

Precis. In the Old World this genus is almost entirely confined to the tropics, but in the New World it extends over North and South America. From the Ethiopian Region 29 species are known, from the Indo-Australian Region 11, some of which have a palaeotropical distribution. Only two species have been found, at least one as a migrant, in the Palaearctic region, viz.:

hierta Fabr. — An abundant species throughout the Ethiopian Region in open country (Williams, 1969); Arabia (Gabriel, 1954); eastward through India (where it is very common; Wynter-Blyth, 1957) to Ceylon and Hongkong (Fruhstorfer, 1912). In the Palaearctic it has only been found in the Lebanon, some 60 years ago. Larsen (1974) thinks that it may have been imported, rather than having made its own way to the Lebanon.

orithya L. — Another palaeotropical species, abundant in open, dry country throughout the Ethiopian Region (Williams, 1969) and extending eastward through Arabia and India to Australia (Gabriel, 1954). It is an immigrant in Iraq, where it prefers oases and river banks (Wiltshire, 1957), but I have not found indications about the origin of the Iraqi immigrants.

Issoria. As delimited by Warren (1956) this genus comprises three species groups, a Palaearctic, an Ethiopian, and a S. American one. Only one of the three Palaearctic species occurs in the W. Palaearctic, viz. *lathonia* L. (Canary Islands, N. Africa and W. Europe to Szechwan and through the Himalayas to Bhutan; Higgins & Riley, 1970; Fruhstorfer, 1912); the other two Palaearctic species are confined to Asiatic mountains.

The Ethiopian species group is composed of three species, viz. *hanningtoni* Elwes, *smaragdifera* Butler, and *excelsior* Butler, distributed over the mountains of E. Africa, south to Malawi, and the Cameroon highlands.

The S. American group numbers five species and is mainly confined to Chili (southward to Tierra del Fuego) and higher parts of the Bolivian and Peruvian Andes (Lehmann, 1913).

The affinities between the species groups are rather obscure. Warren (1956: 390) writes: "It has been shown that the subdivision of *Issoria* is unjustified, the various types of the tenth abdominal segment testify to a close affinity which the world-wide distribution and complete segregation of many species has failed to obliterate". However, such a remark suggests that the groups are conjoined on account of the common possession of plesiomorphous character conditions, a poor basis for monophyly.

Although the phylogenetical affinities are obscure, the geographical affinities seem somewhat clearer. As related genera are absent in Africa but numerous in the Palaearctic Region, the African species group appears to be an Ethiopian offshoot of Palaearctic origin. Moreover, the most usual foodplants of the Palaearctic *Issoria* and related genera, *Viola* species, are also the foodplants of the Ethiopian species. The genus *Viola* is with 400 species mainly distributed in the temperate regions.

It seems possible that the Ethiopian and S. American groups are relics of an once larger, Holarctic group, driven away to outlying districts by a strong development of other (? new) genera (*Argynnis, Brenthis, Boloria,* etc.) in the Holarctic Region, or they could maintain themselves in Africa and S. America, because they had already colonized the mountains of these continents before more successful genera in the Holarctic almost completely replaced their parental stock.

Melitaea. One species, *abyssinica* Oberthür, belonging to the otherwise completely Palaearctic *didyma* group (27 species; Higgins, 1941) is the sole representative of this genus in the Ethiopian Region. It occurs in Ethiopia (Carpenter, 1935) and as a separate subspecies (*scotti* Higgins) in SW. Arabia (Gabriel, 1954).

Ypthima. This genus numbers more than 80 species in the Ethiopian, S. and E. Palaearctic and Oriental Regions, and a single species further east, in New Guinea and Australia (Common & Waterhouse, 1972). The only representative in the W. Palaearctic is *asterope* Klug. It is distributed throughout the Ethiopian Region, in wooded areas, bush, savanna, grasslands (Williams, 1969), and through Arabia and Syria to India, W. and C. China (Gabriel, 1954). As contrasted with what was claimed by Larsen (1974), *asterope* does not reach Australia (cf. Common & Waterhouse, 1972). In the W. Palaearctic, *asterope* occurs as far north as the Adana district in Turkey (Higgins, 1966; Larsen, 1974).

Hipparchia. There is some disagreement on the delimitation of this genus. It has many Palaearctic species. A single species, *tewfiki* Wiltshire, occurs in SW. Arabia (Gabriel, 1954), where it is endemic. Its closest relative is uncertain (possibly *statilinus* Hufn.?), but in view of the distribution of the genus, *tewfiki* undoubtedly has a Palaearctic ancestor.

Lasiommata. Like the related genera, which formerly were united with this genus into the collective genus *Pararge, Lasiommata* is purely Palaearctic, except for two species, *felix* Warnecke, which is confined to SW. Arabia, and *maderakal* Guérin, an endemic species from Ethiopia (Fig. 2). Both species look very much like *maera* L., which extends from N. Africa and W. Europe to the Himalayas and De Lattin (1967) stated that these species are closely related. Indeed, I suppose the specificity of *felix* and *maderakal* is typologically, not biologically based.

Virachola. This genus, which could be considered a subgenus of *Deudorix*, is Indo-African and has 27 species in the Ethiopian Region (Stempffer, 1967). One of these species extends northwards into the Palaearctic:

livia Klug. — An eremic species, known from Tanzania, Somalia, Nubia, Arabia, Israel (Gabriel, 1954), and attaining its northern distribution limit in Lebanon (Larsen, 1974). It is migratory.

Apharitis. This genus was erected by Riley (1925) to receive nine eremic species, distributed from Ghana through the southern Sahara and Arabia to N. India. Their ranges are as follows (data from Riley, 1925, unless stated otherwise):

gilletti Riley. — Somalia.

nilus Hewitson. — S. Sudan to N. Nigeria and N. Ghana.

buchanani Rothschild. — N. Nigeria, S. Sahara.

acamas Klug. — C. Sahara (Ahaggar Mountains), Sudan, Egypt, SW. Arabia, north through Israel, Jordania and Lebanon to Cyprus and Taurus (Hemming, 1932; Larsen, 1974), east to Chitral.

myrmecophila Dumont. — Tunisia; Jordania and SE. Arabia (Hemming, 1932).

epargyros Eversmann. — Kurdistan to Baluchistan and northward to the Kirghis Steppes and Kuldja.

cilissa Lederer. — N. Syria, Kurdistan; Israel (Larsen, 1974).

maxima Staudinger. — N. Syria, Kurdistan.

lilacinus Moore. — Punjab to Assam.

From these data it appears that *Apharitis* is neither an Ethiopian nor a Palaearctic genus, but belongs to the eremic zone between the Ethiopian and Palaearctic Regions and penetrates into those regions.

Tarucus. This Indo-African genus was revised by Bethune-Baker (1918), who distinguished 20 species. Afterwards three species have been added. Stempffer (1967) lists 12 species from the Ethiopian Region. According to Clench (1965) "these small blues are essentially desert or subdesert species". Nevertheless, some species can live in the Palaearctic Region:

theophrastus Fabr. — From S. Spain through N. Africa, Turkey, Arabia and Iraq to India (Higgins & Riley, 1970), Burma and Ceylon (Swinhoe, 1905—10). In

Africa distributed from the Mediterranean to Senegal, N. Nigeria and Ethiopia (Clench, 1965).

rosaceus Austaut. — Algeria, Tunis, and desert oases in N. Africa and Arabia, widely distributed in W. Asia to Iraq and Iran (Higgins & Riley, 1970). In Africa *rosaceus* extends south to Senegal, N. Nigeria and Kenya (Clench, 1965).

balkanicus Freyer. — Coastal regions of Algeria and Tunis, and from the Adriatic coast through the Balkans and Turkey to Lebanon and Iran (Higgins & Riley, 1970). It also occurs in SW. Arabia (Gabriel, 1954). According to Larsen (1974) *balkanicus* occurs through "most of eremic Africa", but I have not found any confirmation of this statement.

The genus extends as far south as S. Africa, where three species occur (Swanepoel, 1953); in the Oriental Region it reaches Borneo.

Lampides. A monotypic genus. Its single species, *boeticus* L., is strongly migratory and occurs with little or no geographic variation throughout the hotter parts of the Old World. In the east it extends to Australia, where it is common (Common & Waterhouse, 1972) and since 1965 it has been found in New Zealand (Laidlaw, 1970). It is common throughout Africa and is found as a resident in S. Europe, but migrants have been observed as far north as N. Germany.

Cyclyrius. Only two species are placed in this genus, viz. *mandersi* Druce, which is confined to Mauritius, and *webbianus* Brullé, which flies in the Canary Islands. This peculiar and apparently relic distribution becomes somewhat more understandable if we know that *Cyclyrius* is thought to be closely related to the next genus, *Syntarucus* (see Stempffer, 1967; Eliot, 1973), which may have replaced *Cyclyrius* in continental Africa.

Syntarucus. Stempffer (1967) lists 11 species from the Ethiopian Region, five of which are restricted to islands. In the Oriental Region a single species, *plinius* Fabr., occurs, from India to Java (Swinhoe, 1910—11; Wynter-Blyth, 1957). One of the Ethiopian species, *pirithous* L., is also found (subspecifically indistinct) throughout S. Europe and much of Turkey. Larsen (1974) considered it an "Afro-eremial species", but it is certainly not strictly "eremial". According to Boorman (1970), it is a common species of forest and savanna areas in W. Africa, and Swanepoel (1953) states that *pirithous* (he used the junior synonym *telicanus*) occurs literally everywhere in S. Africa.

It is interesting to note that no *Syntarucus* species are known from the Canary Islands and Mauritius, where the *Cyclyrius* species are found, although many islands around Africa have been colonized by *Syntarucus* species.

Chilades. There appears to be much disagreement on the delimitation of this genus, also in recent times. Clench (1965) stated: "This small genus of about eight species, most of which are Australian, has two species occurring in Africa...". Stempffer (1967) placed seven Ethiopian species in this genus, although he, in the description of the genus *Freyeria*, stated that *Chilades* occurs from Egypt to the New Hebrides. However, neither D'Abrera (1971) nor Common & Waterhouse (1972) mentioned this genus from the Australian Region. There is only a single Oriental species of which I am sure, viz. *laius* Cramer, as it is the type species of

the genus; it occurs in India, Ceylon, Burma and S. China (Swinhoe, 1905—10).

A single species, *galba* Lederer, is found in the Palaearctic Region. It is confined to the Middle East and has been found in S. Turkey, Lebanon, Jordan, Israel, Arabia, Iraq (Larsen, 1974). According to Wiltshire (1957), it is an oasis and desert insect. Due to the chaotic classification of *Chilades*, it is impossible to state whether *galba* is more closely related to Ethiopian or to Oriental species.

Freyeria. As with the foregoing genus it is obscure which species can be assigned to this genus. In Africa there are two species (Stempffer, 1967). One of them is confined to Madagascar (*minuscula* Aurivillius), the other (*trochilus* Freyer) is widespread in the Ethiopian Region, occurring in the savannas from W. to E. Africa and southwards to the Cape; it is also known from S. Cameroon and Gabon (Clench, 1965). Outside the Ethiopian Region *trochilus* flies from Egypt and Arabia to Ferghana and through the Oriental Region to the Philippines and Australia (Common & Waterhouse, 1972). In the W. Palaearctic it occurs through Lebanon and Iraq north to Turkey and the Balkans. In Europe it is found on barren stony ground (Higgins & Riley, 1970), and Larsen (1974) and Wiltshire (1957) mention comparable habitats in Lebanon and Iraq.

Azanus. Another Lycaenid genus common to the Ethiopian and Oriental Regions. Stempffer (1967) records seven Ethiopian species, while four species are mentioned by Swinhoe (1910—11) from India to Sumatra. One of these species, *jesous* Guérin, occurs in the Palaearctic, in addition to an Afro-Oriental distribution. Its distribution is as follows: Ethiopia to the Cape, Madagascar; in N. Africa in Morocco and Egypt; Arabia to Lebanon; further east in India, Ceylon and Burma (Higgins & Riley, 1970; Larsen, 1974; Wynter-Blyth, 1957). Larsen called it an Afro-eremic species, but he was probably unaware of its occurrence in the Oriental Region.

Zizeeria. A small genus of four or five species (Chapman, 1910; Common & Waterhouse, 1972); two species are confined to the Oriental Region, one to the Australian Region, and the fourth, *knysna* Trimen, is palaeotropical, occurring from S. Africa to Oceania. This widespread species is also found in the W. Palaearctic (Fig. 8). It can be devided into two forms, which only differ in the male genitalia and are, by some authors, considered separate species. These forms are:

knysna Trimen. — Throughout the Ethiopian Region, including Madagascar, Mauritius, Seychelles, north to SW. Arabia in the east (Gabriel, 1954), to Canary Islands and through Algeria and Morocco to northern Spain (Gomez Bustillo & Rubio, 1974) in the west.

karsandra Moore. — E. Algeria, Tunisia, Sicily, Crete (Higgins & Riley, 1970) and from Lebanon to Oceania (Larsen, 1974) and Australia (Common & Waterhouse, 1972).

The habitat of this species is described by Higgins & Riley (1970) as "moist places beside streams", and Wiltshire (1957) observes that "it is not a desert insect, and favours roadsides, paths, lawns and gardens, though not exclusive to such".

Lycaena. There is some disagreement on the subdivision of this genus. In its broadest sense it comprises about 30 Palaearctic (Kostrowicki, 1969) and 16

Nearctic species (Dos Passos, 1964). It is not exclusively Holarctic: there is one species in the mountains of Guatemala, three species occur completely inexplicably in New Zealand (Laidlaw, 1970), and there is a slight Ethiopian representation.

Verity (1943) needed six genera to class the Palaearctic species and his classification was largely, but not entirely, adopted by Higgins & Riley (1970) so far as the European species are concerned. The Ethiopian representatives belong to *Lycaena* s.s., which has about ten Palaearctic species and a number of Nearctic ones. The Ethiopian species are (Fig. 4):

phlaeas L. — Its range comprises almost all of the Holarctic Region. It is a very adaptable species; in the Palaearctic *phlaeas* is found from the oases in the desert-like plains of Iraq (Wiltshire, 1957) to the shore of the Arctic Sea in Norway (Nordström, 1955). In the Ethiopian Region it occurs above 2000 m in SW. Arabia (ssp. *shima* Gabriel) and in the mountains of Ethiopia (ssp. *pseudophlaeas* Lucas).

abottii Holland. — Confined to the highlands of Kenya and N. Tanzania, where it flies in grassy places along streams, etc. The larvae feed on *Rumex* (Williams, 1969), one of the foodplants of *phlaeas*. According to Stempffer (1967), *abottii* could be a subspecies of *phlaeas*.

orus Cramer. — Restricted to S. Africa, where it inhabits the south-western and southern coastal regions as far as Port Elizabeth; it occurs from sea level up to moderate altitude; the larvae feed on *Polygonum* (Clark & Dickson, 1971), one of the foodplants of *phlaeas*.

clarki Dickson. — Also restricted to S. Africa, where it is mainly an inland insect (Clark & Dickson, 1971). Up to 1971 it was considered conspecific with *orus* and the remarks by Swanepoel (1953) about the habitat of *orus* ("a highland butterfly occurring mostly in places where winter is most severe") may refer to *clarki*. The larvae of *clarki* feed on *Rumex* (cf. *abottii* and *orus*).

With regard to the southern extensions of the otherwise Holarctic genus *Lycaena* s.l., Stempffer (1967) remarked: "One can understand how, during the colder geographical [I suppose he meant geological] periods, the genus *Lycaena* managed to reach South Africa by way of the mountains of Abyssinia and East Africa. It is much more difficult to explain how it reached New Zealand, since in Asia it extends no further than the Himalayas and Sze Chuan being effectively replaced by *Heliophorus* in further Asia".

Carcharodus. In its broadest sense this genus comprises about six Palaearctic species; in its most restricted sense it is monotypic, its single species, *alceae* Esper, occurring through most of the western part of the Palaearctic Region, east to C. Asia and N. India. In SW. Arabia it is found as a separate subspecies, *wissmanni* Warnecke.

Spialia. The 27 species of this genus can be classified into seven species groups, which all occur in the Ethiopian Region, while three groups are also represented outside this area (De Jong, 1974b, and in press). Two groups have members in the West Palaearctic Region:

sertorius group (Fig. 10). — Comprised of the species *mafa* Trimen (from S. Africa through E. Africa north to Ethiopia and SW. Arabia), *sertorius* Ochs. (W. Europe and NW. Africa), *orbifer* H.-S. (E. Europe to E. Asia) and *galba* Fabr.

(India to Ceylon and Burma; Hainan). The Palaearctic members, *sertorius* and *orbifer*, are supposed to be the northern offshoot of an originally Ethiopian stock; both can be divided into a number of geographic forms which are believed to reflect the isolation during glacial periods (De Jong, 1974b). The species of this group can usually be found in hot localities, in open and flowery places; I found *mafa* in Kenya up to an altitude of 2000 m.

phlomidis group. — Mainly distributed in the dry regions bordering the desert belt that separates the Palaearctic and Ethiopian Regions. Three species are confined to the region north of the desert belt, viz. *phlomidis* H.-S., *osthelderi* Pfeiffer, and *geron* Püngeler, while the fourth species of this group, *doris* Walker, is found to the north and south of this zone and is, virtually, capable of living in the desert, as far as its foodplant, *Convolvulus lanatus*, grows. In the Ethiopian Region *doris* is known from Sudan, Ethiopia and Somalia. It also occurs in SW. Arabia. In the Palaearctic Region *doris* is found in Morocco and from Egypt to Pakistan. Mainly on the basis of its genitalia *doris* is supposed to be the most recent member of the group (De Jong, 1974b). Although there appears to be a close relationship with the Ethiopian *spio* group, it cannot be stated that the *phlomidis* group has an Ethiopian origin (see also Chapter 3, Summary and conclusions, p. 185). As *doris* seems to be the most recent member of the group and its relatives are Palaearctic, it is concluded that *doris* invaded SW. Arabia and E. Africa from the north.

Gegenes. A small genus of four species. Two species, *niso* L. and *hottentota* Latr., are restricted to the Ethiopian Region, where they are widely distributed; one, *nostrodamus* Fabr., is distributed disjunctly around the Mediterranean, eastward to NW. India and southward to Aden, Omdurman and Kassala, and the fourth, *pumilio* Hoffm., is found over the combined areas of its congeners, but is lacking from Tunisia to the Sinai. All species are usually met with in hot and dry localities, and *nostrodamus* and *pumilio* appear to be the most eremic species, which may count for the fact that they occur in the Palaearctic as well as the Ethiopian Region and have a patchy distribution around the Mediterranean. Although the Ethiopian species (*hottentota* and *niso*) can live in dry conditions, they are usually found in more or less grassy places. Indeed, in E. Africa *niso* is perhaps the commonest species of Hesperiidae and I found it in Kenya most numerous along paths in more or less wooded areas. Possibly their preference for grassy places has forced *niso* and *hottentota* to remain restricted to Africa south of the Sahara.

Recently, Larsen (in litt.) found differences between the East and West Mediterranean *pumilio* populations and he thinks these populations to be specifically distinct. This interesting observation has also some bearing on the reconstruction of the geographic history of the genus. On the (unfirm) basis of the distribution of related genera (cf. Evans, 1937, 1949) I have concluded that the genus originally formed part of the old, Tertiary steppe fauna that invaded Africa from the east. As the extant species seem to fall apart into two groups, viz. *pumilio/nostrodamus* and *niso/hottentota*, there appears to have been an Ethiopian and a South Palaearctic development of the genus, which may have been initiated by the desiccation of the area that is now covered by the Saharo-Arabian desert. In this reconstruction the differentiation of *pumilio* in the Mediterranean area may

be the result of glacial isolations, and both *pumilio* and *nostrodamus* are northern invaders in Africa.

An alternative hypothesis, adhered to by Larsen, assumes that *pumilio* is an Ethiopian species that invaded the Mediterranean along two routes, giving rise to an East and a West Mediterranean form. If the ancestor of the *pumilio/nostrodamus* stock was Ethiopian, also *nostrodamus* is an Ethiopian element in the Palaearctic and one could imagine that *Gegenes* expanded twice to the Mediterranean, the first time bringing the ancestor of *nostrodamus* to the north, the second time giving rise to the two different *pumilio* forms. This reconstruction sounds very plausible, but does not take into account that the *pumilio/nostrodamus* ancestor must have originated somehow and somewhere. As the *Gegenes* species can live in steppe-like habitats, the genus has undoubtedly formed part of the steppe fauna that in Tertiary times was distributed from Africa to India, whatever the geographic origin of the *Gegenes* ancestor. In that case, however, it is much more easily imaginable that *pumilio/nostrodamus* originated north than south of the Sahara (see above). Consequently, I consider provisionally both *pumilio* and *nostrodamus* northern invaders in Africa. I cannot consider the wide distribution of *pumilio* south of the Sahara (ssp. *gambica* Mab.) an objection to this hypothesis, for why should not a steppe species expand itself so widely over Africa?

Borbo. A palaeotropical genus; 17 species are restricted to the Ethiopian Region, three are only found in the Indo-Australian area, and one species, *borbonica* Boisd., is distributed throughout the Ethiopian Region, in Madagascar and various islands in the Indian Ocean (Bourbon is type locality), in N. Africa (Morocco, Algeria, Egypt), the Middle East (Syria, Lebanon, Israel), and is also found in Spain, in Gibraltar and Tarragona (Gomez Bustillo & Rubio, 1974). The Mediterranean populations have been distinguished as ssp. *zelleri* Lederer. *B. borbonica* is a rather eclectic species which can live in eremic as well as in more humid and wooded areas. I found it in W. Kenya along paths in the Kakamega Forest.

Pelopidas. This genus is mainly Indo-Australian, but among its nine species two (*mathias* F. and *thrax* Hbn.) are found in the Ethiopian as well as in the Oriental Region and these species are the sole representatives of the genus in Africa. Only *thrax* reaches the W. Palaearctic: Turkey (Higgins, 1966), Syria, Lebanon (Larsen, 1974), Jordan (Hemming, 1932), Cyprus, Israel (Evans, 1949); further from Egypt through Arabia and Iraq to NW. India, Burma and Malaya (Evans, 1949), and through most of the Ethiopian Region (Evans, 1937). In the W. Palaearctic the same subspecies (ssp. *thrax* F.) occurs as in NW. India, the Ethiopian subspecies is different (ssp. *inconspicua* Bertolini). It is a known migrant (Larsen, 1974), but that does not mean that it is not resident in the W. Palaearctic. As *B. borbonica, thrax* seems to be a species that has not a very restricted habitat preference.

3. THE AFFINITIES BETWEEN THE WEST PALAEARCTIC AND ETHIOPIAN BUTTERFLY FAUNAS

From the data given in Chapter 2 it is obvious that the Palaearctic-Ethiopian affinity cannot be simply described as a north-south connection, but that it is of a

rather complex nature. In this chapter we will try to unravel the various types of affinities. The first division to be made is into direct and indirect affinities.

The term "direct affinity" is applied to those cases which concern a penetration from region A into region B, disregarding a possible secondary radiation in region B. In the present instance two such direct affinities are possible, viz. a penetration from the Palaearctic into the Ethiopian Region and vice versa.

By the term "indirect affinity" is meant that region A or B, or both, received the taxon which it has in common with the other region, from a source outside the other region. In some cases this source can be indicated (allowing a subdivision of this category), in other cases taxa are placed under this heading by lack of knowledge.

Direct affinities

Palaearctic influence in the Ethiopian Region

The species of this group are listed in Table 2. Some features of this group are:

a. all species belong to genera which are not represented in the Oriental Region, or at most penetrate slightly into that region (*Pieris, Colias, Gegenes*);

Table 2. Species of (ultimately) Palaearctic origin in the Ethiopian Region. An asterisk indicates that the species is not specifically distinct from Palaearctic species

	SW. Arabia	E. Africa	S. Africa
Pieris brassicoides		×	
Pontia daplidice	×	×	
* glauconome*	×	×	
distorta		×	
helice		×	×
Euchloe belemia		×	
* falloui*	×	×	
Colias erate	×	×	
electo	×	×	×
Issoria hanningtoni		×	
smaragdifera		×	
excelsior		×	
Melitaea abyssinica	×	×	
Hipparchia tewfiki	×		
Lasiommata maderakel		×	
felix	×		
Tarucus balkanicus	×		
Lycaena phlaeas	×	×	
abottii		×	
orus			×
clarki			×
Carcharodus alceae	×		
Spialia dorus	×	×	
Gegenes nostrodamus	×	¹)	
* pumilio*		×	×

¹) occurs in Sudan

b. most Ethiopian representatives are conspecific with Palaearctic species or are so closely related that they can be considered to form a superspecies together with Palaearctic species;

c. in the Ethiopian Region most species are confined to the north-eastern, eastern and/or southern part, and no species are confined to W. Africa;

d. none of the species are forest species, though they may fly in close proximity to the forest; for the rest, their habitat preferences are divergent, ranging from eremic (e.g., *Euchloe falloui*) to montane grasslands (e.g., *Pieris brassicoides*).

Ethiopian influence in the Palaearctic Region

There is only a small number of originally Ethiopian species occurring in the Palaearctic Region, but as will be shown it is impossible to delimit this group precisely. The species are listed in Table 3. Their common features are:

a. all species belong to genera which have at least one endemic species in the Oriental Region;

b. all species fly north as well as south of the Sahara and the northern populations are usually subspecifically not differentiated from the southern ones (*Spialia sertorius* and *orbifer* are exceptions; they are considered to form a superspecies with the Ethiopian *mafa* and the Oriental *galba*);

c. in the Palaearctic the species are confined to the Mediterranean area (again, *Spialia sertorius* and *orbifer* are exceptions);

d. they are no forest species, but for the rest their habitat preference is divergent. Generally speaking the species live in Africa in various types of savanna country. The pierid and lycaenid species are the most eremic ones.

Table 3. Species in the Palaearctic Region originating from the Ethiopian Region. An asterisk indicates that the species is not specifically distinct from its Ethiopian relative, two asterisks indicate that the species occurs with different subspecies in the Palaearctic and Ethiopian Regions

	West Mediterranean	East Mediterranean
**Colotis evagore*	×	
* calais		×
* chrysonome		×
Catopsilia florella p.p.	[1])	[2])
Danaus chrysippus alcippus	×	[2])
**Charaxes jasius*	×	×
Virachola livia		×
Syntarucus pirithous	×	×
Zizeera knysna knysna	×	[2])
Spialia sertorius	×	
orbifer		×
**Borbo borbonica*	×	×

[1]) only in Canary Islands
[2]) see Table 4

Of the listed species we can be reasonably sure that they are Ethiopian intruders in the Palaearctic Region, as they otherwise occur only in Africa (except *Spialia*). Among the species listed in Table 3, four have an Indo-African distribution. Their

Ethiopian origin has been concluded from their geographic variation, except *Catopsilia florella,* which has no subspecies and of which the Canary Islands population can only have originated from W. Africa. There are, however, more species with an Indo-African distribution which also occur in the Palaearctic Region, but without a subspecific indication as to their geographic origin. For that reason they will be dealt with in the next paragraph.

Indirect affinities

Indo-Ethiopian and eremic species

As it appears impossible to divide sharply between species with an Indo-Ethiopian and an eremic distribution, these species (so far they occur in the Palaearctic Region) have been listed together in Table 4. Their common feature is

Table 4. Species in the Palaearctic Region with an Indo-Ethiopian or eremic distribution

	W. Medi-terranean	E. Medi-terranean	Africa S. of equator	migratory
Colotis phisadia		×		
fausta		×		×
Anaphaeis aurota		×	×	×
Catopsilia florella	¹)	×	×	×
Danaus chrysippus chrysippus	¹)	×	×	×
Hypolimnas misippus		×	×	×
Precis orithya		×	×	×
Ypthima asterope		×	×	
Apharitis acamas		×		
myrmecophila	×	×		
Tarucus theophrastus	×	×		
rosaceus	×	×		
Lampides boeticus	×	×	×	×
Chilades galba		×		
Freyeria trochilus		×	×	
Azanus jesous	×	×	×	
Zizeeria knysna karsandra	×	×	²)	
Pelopidas thrax thrax		×	×	×

¹) see also Table 3
²) in the Ethiopian Region only *Z. knysna knysna*

that it is improbable that they have an Ethiopian or Palaearctic origin. For some species (*Colotis fausta, Pelopidas thrax*) an Oriental origin appears obvious. For other species the region of origin is quite uncertain and it is possible that all species belong to the fauna that has always lived in the contact area between the Palaearctic, Oriental and Ethiopian Regions, not a mixed fauna, but a more or less independent, intermediate fauna (without sharp boundaries). This is most obvious in the eremic species, as they are confined to the said region. The less confined to an eremic habitat, the larger is the distribution, and some species can live in such a variety of habitats, including the eremic, that they could extend their range throughout the warmer parts of the Old World (e.g., *Danaus chrysippus,*

Hypolimnas misippus, Lampides boeticus). Whatever their place of origin, none of these species can now be considered a Palaearctic intruder in Africa or an Ethiopian intruder in Eurasia.

Two other features call for attention, viz. the small number of species of this category in the W. Mediterranean and the large number of migratory species. The latter feature may be partly responsible for the slight subspecific differentiation of the species. The occurrence of two of these species in the W. Mediterranean, viz. *Catopsilia florella* and *Danaus chrysippus chrysippus*, appears to be a direct result of their migratory habit. Apart from these two species only five species of Table 4 occur in the W. Mediterranean, while all species are known from the E. Mediterranean (none of the species occurs outside the Mediterranean except the migratory *Lampides boeticus*). A possible historical explanation for this difference is given in Chapter 4.

Remaining genera

Five genera remain to be dealt with. Two of them, viz. *Papilio* and *Neptis*, are very rich in species in tropical environments, while few species occur in temperate regions. Whatever their geographic history may have been, there are no indications that they crossed the eremic zone between the Palaearctic and Ethiopian Regions in more or less recent times as no species occur north as well as south of the Saharo-Arabian desert zone. It is possible, if not probable, that the W. Palaearctic members of these genera are originally invaders from the E. Palaearctic (and neighbouring Oriental) Region.

The distributions of the genera *Libythea* and *Cyclyrius* show a relict character and little or nothing can be said on their history.

The genus *Vanessa* is the only one in this group that has the same species (*cardui*) flying in both the Palaearctic and Ethiopian Regions. Although this very strongly migratory species seems to cross the Sahara rather regularly to the north, it is very unlikely that it should be considered an Ethiopian intruder in Europe. Although its geographic origin is uncertain, it may be suggested that *cardui* is a New World species that by its strong migratory behaviour conquered the world.

Summary and conclusions

Summarizing, four kinds of relationship between the West Palaearctic and Ethiopian Regions can be distinguished:
a. by southward traverse across the Saharo-Arabian desert zone,
b. by northward traverse across the Saharo-Arabian desert zone,
c. through the Oriental Region,
d. through the eremic fauna.

Apparently the Sahara has been successfully crossed several times by various species, from north to south and vice versa. Taking the view that generally speaking the existence of species common to the regions north and south of the Sahara indicates a more recent contact than that of common genera without common species, the traverses seem to cover a long period. The more remarkable

is the very small number of successful traverses. Successful north-south traverses number about 17 (cf. Table 2) and most traverses are of such a recent age that the species concerned scarcely had time for differentiation (although only ten originally Palaearctic species in the Ethiopian Region are considered conspecific with Palaearctic species). If we bear in mind that the West Palaearctic comprises more than 400 butterfly species, it is apparent that the Sahara is an efficient barrier for the West Palaearctic butterfly fauna in general.

For the Ethiopian butterflies the Sahara appears to act as a still stronger barrier. Successful northward traverses number only twelve (cf. Table 3). As the Ethiopian butterfly fauna comprises almost 2700 species, it is evident that a successful crossing is a very rare event (but in Chapter 4 it will be shown that unsuccessful crossings may have been rather frequent). In all cases the same species occurs north as well as south of the desert zone and the species are confined in the Palaearctic to the Mediterranean (with the exception of *Spialia sertorius/orbifer*). This suggests that the average age of the northward traverses is still younger than that of the southward ones.

Thus there appear to exist two remarkable differences between the southward and northward traverses, viz.:

a. in relation to the total number of butterfly species in the West Palaearctic and Ethiopian Regions the southward traverses are much more frequent than the northward ones;

b. judged from the differentiation of the species after the traverse the southward traverses cover a much longer period than the northward ones.

A possible explanation for these differences is given in the next chapter.

The Indo-Ethiopian genera pose a separate problem. Not all of these genera have representatives in the W. Palaearctic. The complex nature of the Indo-Ethiopian relationship falls outside the scope of this paper, but in the next chapter a few words have to be said on this subject in order to get a better insight in the Euro-Ethiopian affinities.

4. Historical aspects

In this chapter we will try to relate the data amassed in the foregoing chapters to ecological changes in the northern part of Africa in the past. As the Euro-Ethiopian affinities in the butterflies are mainly at the species level, we are primarily interested in the ecological changes that took place during the Pleistocene. Affinities at the genus level may point to an older, Tertiary connection. Very little is known of this period and various authors do not always agree. Nevertheless, the little that is known may help to explain the distribution patterns found.

Ecological history of the northern half of Africa and the Arabian peninsula

Tertiary

For our purpose it does not seem relevant to consider the period prior to the Miocene as it is hardly believable that a contact broken since then is at present still discernible at the genus level.

From Middle Miocene to Late Pliocene there was a connection with the Oriental Region via Arabia. The Red Sea in its present form came into existence only at the end of the Pliocene or the beginning of the Pleistocene; prior to that time it was a large inland sea (Ekman, 1953). As the Persian Gulf also appears to be rather recent and the climate in this area in Miocene and Pliocene was often more humid than at present (e.g., at the end of the Miocene and various times in the Pliocene Egypt has experienced periods of considerable rainfall, see Moreau, 1952), a close contact between and intermingling of the Oriental and Ethiopian faunas was possible. This intermingling was largely unidirectional and consisted mainly in a large invasion of Oriental faunas (De Lattin, 1967). In the Pliocene the correspondence has been still larger than at present, as many groups became extinct in the Oriental Region (shown by the famous fossil Siwalik fauna of N. India).

I wonder if it is correct to speak of Oriental species invading Africa, as is usually done. It concerns mainly steppe species which lived in a region that is now partly Oriental, partly Palaearctic. The uplift of the Himalayas (of which the Siwalik Range forms the southern border), the main boundary between the Palaearctic and Oriental Regions, "is believed (...) to have taken place in four major impulses, respectively during the Eocene, the Middle Miocene, the Upper Pliocene and in the Late Pleistocene" (Mani, 1968). This means that it is not relevant to speak of a Palaearctic and an Oriental Region as biogeographical regions in the Tertiary. Thus, it is misleading to speak of an Oriental invasion into Africa, and it seems more suitable to term it an Asiatic invasion.

More temperate Asiatic species, especially those which could not live in a steppe or savanna environment, had at this period no chance of reaching Africa as the mountains by way of which they could cross the steppe region were still in the process of uplifting and there were not yet mountains in East Africa high enough to support temperate species.

The progress of the Alpine orogeny in Late Tertiary and especially the gradual rise of the Taurus-Armenia-Zagros mountain system, the falling temperature and the opening of the southern end of the Red Sea (not before the middle of the Pliocene; Ekman, 1953), must have hampered the free exchange of steppe species between Asia and Africa. Nevertheless, during humid periods the passage, though difficult, must have been possible.

There is no full agreement on the Tertiary connections between Africa and Europe in the W. Mediterranean. According to Moreau (1966) there was a landbridge in the Tunisia-Sicily area in the Pliocene. Besides such a landbridge Verity (1940) mentioned a direct connection between Sardegna and Africa in the early Pliocene, but it is not clear how far such a connection is supported by geological evidence.

Although Moreau (1966) stated that there is no evidence of a connection across the Straits of Gibraltar, Ekman (1953) postulated a Middle Tertiary landbridge between Cape Spartel and Cape Trafalgar, although in the Pliocene the Mediterranean became connected to the Atlantic, subsequently through the valley of the Guadalquivir, the valley of Fez and at last across the Straits of Gibraltar. A similar sequence of events was given by Verity (1940) and Kostrowicki (1969). It is

clear that such a connection in this area cannot have been of much importance as a direct passage, as only those species occurring in the northernmost tip of NW. Africa when it was conjoined to Spain, could freely move into Africa when this part became connected to the rest of NW. Africa. But apart from such a connection, the Straits of Gibraltar are only a narrow gap (at present 13 km), and anyone who from Tarifa, the southernmost point of Spain, has looked at the mountains of Tanger will be convinced that in due course many species must have been able to cross the gap.

In the meantime the Atlas Mountains were uplifted, rendering temperate species a possible habitat far to the south. However, during the Tertiary the lowland was probably still too warm to give temperate species the opportunity to expand to the south. Moreover, the Sahara south of the Atlas Mountains would have been a strong barrier for temperate species, although it may have been covered over large areas by mediterranean shrub and savanna-like vegetation, possibly continuously so along the Atlantic coast to the W. African savannas. But warmth-loving species of open formations may have been able to cross the Sahara by this way (to the north as well as to the south), thus forming a connection between the European and Ethiopian faunas.

In sum, interchange of species between the W. Palaearctic and Ethiopian Regions during the Miocene and Pliocene was possible through Arabia and the Middle East and, probably to a lesser extent, across the W. Mediterranean and through NW. Africa. Only species which could live in a steppe or savanna-like environment could make use of these connections.

The above description suggests that we know a lot of the Late Tertiary ecology in the area concerned, but considering that this period covered about 25 millions of years during which large mountain massifs were uplifted and ecological conditions must have changed at a large scale, it is clear that we know extremely little.

Pleistocene

About the relatively short Pleistocene period (about 2 millions of years; considered here to extend up to the present day, after Moreau, 1966, and Hamilton, 1974) we are rather better informed, though most data refer to the last 30,000 years.

The glaciations of the Palaearctic brought many temperate species far to the south where they could survive warmer interglacial periods in the S. Palaearctic mountains. Thus, an ecologically wider array of species stood, as it were, waiting to cross the Sahara as soon as conditions became favourable.

At present the Sahara is too dry to be crossed by Palaearctic as well as Ethiopian species. During a more humid period an interchange of species living in steppe and savanna and perhaps mediterranean shrub would be possible, but for species not capable of living in such an environment a lower temperature is required. Recent investigations, particularly pollen analysis, have revealed that there have, indeed, been colder and more humid periods. The history of the vegetation of East Africa was summarized by Van Zinderen Bakker (1971) and Hamilton (1974). It appears that from 30,000 to 25,000 BP (Kalambo Interstadial,

corresponding with the European Paudorf Interstadial) the temperature was about 2° C lower than at present. The temperature decreased between 25,000 and 12,500 BP to 6° C lower than now. This period is known as the Kenya Glacial and coincides with the last maximum of the Würm Glaciation in the Palaearctic. After a rapid increase the temperature c. 10,500 BP was similar to today. A further synchronization in the temperature fluctuation between Europe and East Africa is the occurrence of a short cold phase just before the Postglacial Climatic Optimum, about 4500—7500 BP (Neolithic), when temperatures were about 2° C higher than today.

This synchronization suggests that similar fluctuations took place in the intervening area. This is very important. The lower limit of the montane zone in East Africa, at present at 1500 m, is supposed to have been depressed at least by 1000 m during the maximum of the Kenya Glacial and Moreau (1966) calculated that even only 12,000 BP, with a temperature 2.5° C lower than today, the lower montane limit would have been at 1000 m. If we suppose that a similar descent of the montane zone took place in the area between East Africa and the Palaearctic, the enormous impact on the distribution of montane habitats is easily seen from the surface relief shown in Fig. 1. In fact an almost continuous montane block was
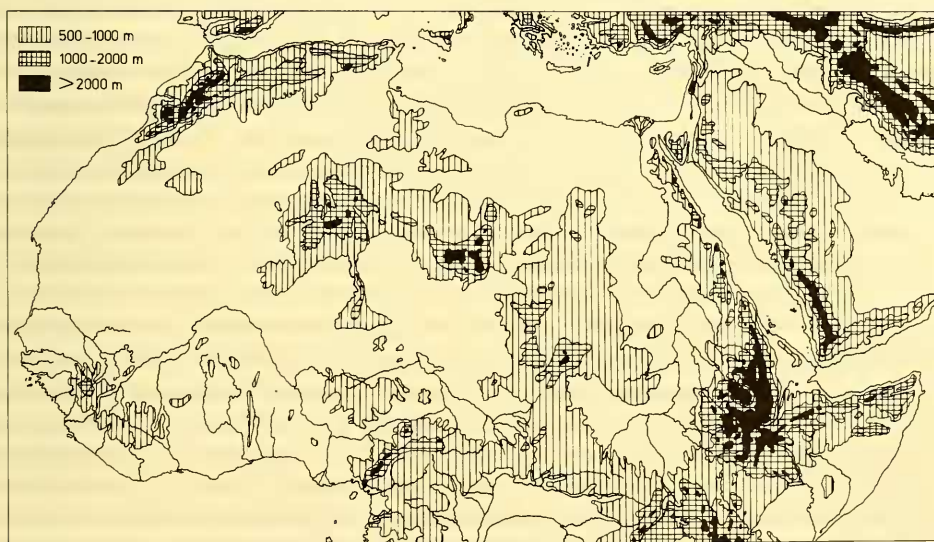

Fig. 1. Surface relief in northern Africa

formed from Asia Minor to East Africa, and from NW. Africa diagonally across the Sahara to Central Africa. Indeed, pollen analysis has shown that the Ahaggar Massif during much of the later part of the last glaciation was clothed with a rich mediterranean vegetation and even the European lime (*Tilia*), now absent in N. Africa, occurred there (Moreau, 1966).

There is, however, one factor which must have greatly influenced the availability of montane habitats for Palaearctic species trying to extend their range

southward, viz. humidity. Hamilton (1974) observed, that at least in the East African mountains the last glacial was dry, contrary to the common opinion that it was a pluvial period. Moreover, according to Moreau (1966) Arabia has probably never been better than semiarid at any time during the Pleistocene, except the mountain areas of Yemen and Gebel Akhdar and the somewhat elevated southern rim of Arabia, where wooded steppe and savanna may have existed, possibly with patches of dry evergreen forest, during glaciations and the humid Neolithic.

Although the duration, extension and chronology of dry and humid periods are still largely unknown, it is clear that drought must have hampered the southward extension of Palaearctic species, if it occurred during the only periods the temperature was low enough for such an extension, i.e. during glacial periods.

For Ethiopian species trying to extend their range northward, drought as well as low temperatures would have been unfavourable. How far the warm interglacial periods have been favourable for northward extensions is unknown at present (apart from a humid period in the latter Middle Pleistocene; Moreau, 1963), but at least postglacially there has been a favourable period, viz. the humid period during the Neolithic, in Europe known as the Postglacial Climatic Optimum or the Atlantic (cf. Moreau, 1955). This humid period, with a temperature about 2° C higher than now, attained its maximum about 5,000 years BP. At that time the western Sahara (and also the mountains of Aïr and Tibesti) was covered by mediterranean vegetation (scrub and dry woodland) up to the southern limit of the present Sahara, where it was in contact with the Ethiopian savanna vegetation (Moreau, 1966). Braestrup (1947) pictured the rivers at that time running across the western Sahara. It is clear that especially the coastal belt along the Atlantic requires only a small degree of climatic improvement in order to become viable as a passage for northern and southern species. The area north-east of the line Tripoli-Khartoum, however, appears to have always been drier and during the Neolithic only the Nile Valley could act as a corridor in this area (Moreau, 1963). However, the Neolithic period is believed to have been humid in the Sudan and Ethiopia and Moreau (1966) mentioned for Arabia, at least for its southern part, a somewhat richer vegetation, especially in mountainous areas, during this period.

For temperate Palaearctic species trying to go southward the Postglacial Climatic Optimum must have been a bad period. As a consequence of the higher temperature (about 2° C) the lower limit of the montane zone was about 400 m higher. Mountains below 1900 m lost their montane habitat and their function as stepping stones, montane habitats became more isolated and the land in between too hot.

By a sudden deterioration late in the Neolithic, caused by unknown factors, the entire mediterranean vegetation in the western part of the Sahara became extinct and from that time on the present bare condition of the western Sahara was developed. A similar condition has existed earlier in the Pleistocene, as at some stage in the late Pleistocene, prior to 22,000 BP the dunes of the Sahara extended even 300 miles south of the present limit of moving sands in West Africa. It is obvious that the present and similar conditions do not facilitate the passage in both directions.

To summarize the Pleistocene vicissitudes, it can be said that during glaciations,

conditions were favourable for a southward traverse, as far as drought did not prevent it. For the last time such conditions existed from about 25,000 to 18,000 BP. Northward traverses were mostly feasible during humid periods, the last of which occurred only about 5000 BP.

The distribution of mountain ranges suggests that the route from the Middle East to the Ethiopian highlands and further south was much easier for temperate species than from the NW. African mountains southward. It is not clear whether a western or an eastern traverse was easier for Mediterranean and Ethiopian species; possibly both traverses were equally easy (or difficult), though not necessarily at the same time.

The direct West Palaearctic - Ethiopian affinities

The southward traverse

The Palaearctic species in the Ethiopian Region are largely absent from West Africa, suggesting that these species used mainly the eastern traverse. It should, however, be borne in mind, that East Africa offers the best opportunities for more or less temperate species to survive in its large mountain areas, and the possibility that also the western traverse was used but the species became extinct there, cannot be ruled out in advance. Indeed, there are indications that some species crossed the Sahara in its western part, but if they ever reached the Ethiopian Region, they died out entirely there. The southward movement in the western traverse is shown by the species at present occurring in the mountain areas in the Central Sahara, viz. Ahaggar (3000 m), Aïr (2000 m), and Tibesti (almost 3500 m). Table 5 gives an impression of the butterfly composition of these mountains. Although the data of these areas are incomplete, it is remarkable that in Tibesti, at the greatest distance from the Atlas Mountains, still six species of the families Pieridae and Nymphalidae occur that can be considered northern immigrants. Bernardi (1962) also listed *Vanessa cardui* as a Palaearctic species in Tibesti, but to me the geographic history of *cardui* seems obscure; moreover, the lack of subspecific variation makes it impossible to decide on the origin of the Tibesti population.

Four out of the six Palaearctic species in Tibesti have also been found in the Sahara between the Atlas Mountains and In-Salah (= Aïn-Salah), more than halfway Ahaggar, mainly in river beds and oases (Rothschild, 1913). These species have also been found in the northern part of Rio de Oro (Bernardi, 1966). One of them, *Pontia glauconome,* is actually an eremic species. It is obvious that a more humid period can easily bring these species across the Sahara and their isolation in the mountains in the Central Sahara (if they are isolated there at all) is not older than about 5000 years (Postglacial Climatic Optimum). This may also count for the fact that they are subspecifically indistinct from specimens from Algeria.

Of the two remaining Palaearctic species in Tibesti, *Vanessa atalanta* is a well-known migrant, as is the cosmopolitan *Vanessa cardui.* It is not impossible that at least the latter species crosses the Sahara regularly in present times.

Melitaea didyma appears to be the only species which requires a colder period for

Table 5. Composition of butterfly species in various regions of the Sahara. Data extracted from Rothschild (1913, 1915, 1921), Riley (1934), Bernardi (1962) and Bernardi & Stempffer (1951)

	NW. Sahara	Ahaggar	Aïr	Tibesti	Palaearctic
Papilio machaon	×	×			×
Pieris rapae	×				×
Pontia daplidice	×	×	×	×	×
glauconome	×	×		×	×
Euchloe ausonia		×			×
falloui	×	×			×
belemia	×				×
Elphinstonia charlonia	×	×		×	×
Colotis calais			×		
phisadia		×	×	×	
chrysonome		×	×	×	
halimede			×	×	
eupompe			×		
liagore			×	×	
evagore	×		×		
aurora			×	×	
evippe				×	
eris				×	
Pinacopteryx eriphia				×	
Calopieris eulimene				×	
Anaphaeis aurota				×	
Nepheronia buqueti			×		
Colias croceus	×			×	×
Catopsilia florella			×	×	
Eurema brigitta			×	×	
Vanessa atalanta				×	×
cardui	×	×	×	×	
Precis oenone				×	
Byblia ilithyia			×		
Melitaea didyma				×	×
deserticola	×				×
Danaus chrysippus	×		×	×	
Ypthima asterope			×		
Virachola livia		×	×		
Iolaus nursei			×		
Apharitis acamas		×			
Anthea crashayi				×	
Cacyreus lingeus				×	
Castalius cretosus			×		
Tarucus theoprastus	×	×			
rosaceus			×		
Lampides boeticus			×		
Chilades eleusis			×		
Azanus ubaldus			×		
Zizeeria knysna	×		×		
Aricia cramera	×				×
Lycaena phlaeas	×				×
Gegenes nostrodamus	×				×

extending its range so far to the south (the mention of this species from the Sahara between the Atlas and Ahaggar by Rothschild, 1913, concerns the related species *M. deserticola*, see Higgins, 1941). It is however surprising that this geographically confusingly variable species in Tibesti occurs in a form which is subspecifically indistinct from the Algerian form, thus suggesting a much more recent contact than the seemingly required Last Glacial.

From Ahaggar three Palaearctic species are known that have not been found in Tibesti, viz. *Papilio machaon, Euchloe ausonia* and *Euchloe falloui*. Subspecifically they are scarcely or not at all distinct from the Algerian representatives of the respective species, suggesting that they reached the Ahaggar in relatively recent times. As in the case of *Melitaea didyma* in Tibesti we are forced to suppose a more recent range extension than during the Last Glacial. As *P. machaon* and *E. falloui* have actually been found in the NW. Sahara (Rothschild, 1915), they may even now reach the Ahaggar at times. The Postglacial Climatic Optimum must have been favourable for their range extension, though the temperature was higher than at present, as they could follow a route mainly over higher land (500—1000 m) (Fig. 1). In the same way *Euchloe ausonia* and *Melitaea didyma* may have reached the Central Saharan mountains, though for them the passage was more difficult and their occurrence so far to the south appears the result of a chance colonization.

There are no traces of a penetration from NW. Africa still further across the Sahara. About 400 km south-east of Tibesti extends the Ennedi mountain range. No Palaearctic species are known from this area. except the eremic *Pontia glauconome* (Bernardi, 1964).

Although the Aïr mountains are much closer to Ahaggar than Tibesti, they have only a single Palaearctic species, viz. *Pontia daplidice*. This paucity may be attributed to their much smaller extent and less elevation. It is noticeable that there are no traces left of butterflies colonizing the Central Saharan mountains during the Last Glacial. If they ever did, they died out entirely.

While in the Saharan mountains the affinities with the Palaearctic Region are at the species and even subspecies level, the picture in East Africa is quite different. Of the 25 species in the Ethiopian Region thought to be ultimately of Palaearctic origin (Table 2), less than half (11) are considered specifically indistinct from Palaearctic species and only four or five of them are regarded subspecifically identical. This suggests that the contact with East Africa is at least partly of a much older date, and the various grades of relationship between the Ethiopian and Palaearctic members (subspecific, specific, superspecific, generic) indicate a repeatedly broken contact.

The generally older age of the Palaearctic-E. African contact is due to the fact that only few of the species concerned could use this eastern traverse across the eremic regions during the humid Neolithic, viz. *Pontia daplidice* and *glauconome, Euchloe belemia* and *falloui, Colias erate* and *Tarucus balkanicus*. Except the last one, these species have also been supposed to have extended their range southward during the same period through the western traverse. Their slight differentiation in the Ethiopian Region is apparently due to the rather recent date of their isolation.

Fig. 2
Lasiommata maera group
  L. maera
  L. felix
  L. maderakal

Fig. 3
Superspecies Pieris brassicae
  P. brassicae
  P. brassicoides

Fig. 4
Lycaena phlaeas group
  L. phlaeas
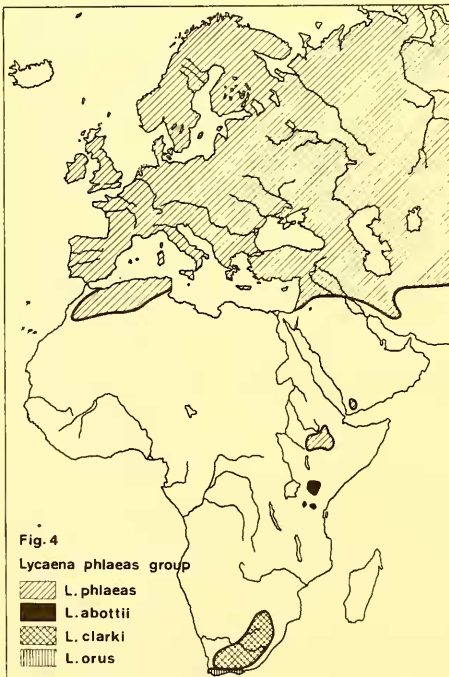 L. abottii
  L. clarki
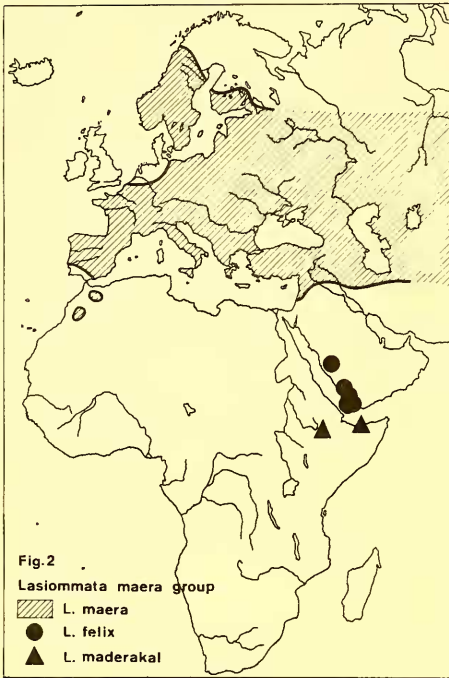 L. orus

Fig. 5
Pontia helice

Fig. 2—5. Butterfly species with Palaearctic ancestry in the Ethiopian Region

As the other species need a lower temperature, their isolation must date back at least as far as the last phase of the Last Glacial, i.e. 18,000—25,000 years ago. The differentiation of the *Lycaena phlaeas* group can only be attributed to at least two subsequent southward movements, the first of which (giving rise to *L. orus/clarki*) may also have brought *Pontia helice* to S. Africa. It is impossible to date these movements more or less exactly, but there is no reason to consider them otherwise than coinciding with various phases of the Last Glacial or with an earlier Glacial. The systematic isolation of the *Issoria hanningtoni* group may also be due to a long geographic isolation, from before the Last Glacial.

The history of *Pontia distorta* is still obscure. It is confined to the dry savanna of Somalia and Kenya and may have come there during a dry period across the Ethiopian mountains, but before further suggestions are made, it is advisable to clear up the relationship of *distorta* to other *Pontia* species.

A glance at Fig. 1 shows that in the eastern traverse two routes were available for the temperate species (i.e. the species which needed a cold period for their southward movement), viz. east and west of the Red Sea. The eastern route with its large mountainous areas seems to offer the best opportunities, though using this route the species had to jump the southern end of the Red Sea and a lowland area. From the species known to occur in the SW. Arabian mountains it is clear that many species used this route indeed and it seems possible that most Palaearctic species which reached Ethiopia, did so by way of this route. For species that needed a humid rather than a cold period for range extension the jump over the southern end of the Red Sea must have been still easier.

In table 2 are indicated the species of Palaearctic origin occurring in SW. Arabia. The data are extracted from Gabriel (1954), who mentioned 18 Palaearctic species in SW. Arabia, but he did not mean to state a geographic origin, only to indicate that the species concerned also occurred in the Palaearctic Region. Two of the species listed in table 2 belong to genera which are unrepresented in Africa south of the Sahara (*Eumenis, Carcharodus*). Apparently, it was too difficult for these species to make the jump to the Ethiopian highlands (or they became extinct there). The other species are represented by closely related species (*Pararge felix*), or subspecies (*Melitaea abyssinica, Lycaena phlaeas*) or by identical subspecies (remaining species) in Ethiopia. These data strongly suggest, that the gap between the SW. Arabian and Ethiopian mountains was not insurmountable for many Palaearctic species (see also the next paragraph and Chapter 5, the paragraph on the Red Sea). Of the Palaearctic species in East Africa only *Pieris brassicoides* and the *Issoria hanningtoni* group have no relatives in SW. Arabia, so that it is quite impossible to say which route they used to reach Ethiopia.

Summary and conclusions. Two traverses have been available for a southward movement across the Saharo-Arabian desert zone, viz. a western traverse, from the Atlas Mountains across the W. Sahara and the mountains of the C. Sahara, and an eastern traverse, at either side of the Red Sea. During the cold Glacial Periods and phases, the last of which reached its maximum only 18,000—25,000 years ago,

temperate species could extend their ranges southward through the mountains of the western and eastern traverses, but only traces of a repeated use of the eastern traverse have been left. The western traverse was a dead-end road as there was no link with an Ethiopian mountain range that could support temperate species during warmer times. Even in the C. Saharan mountains no traces are left of glacial range extensions by butterflies from the north.

The very low number of glacial invaders in East Africa and SW. Arabia (about eight) can have various causes:

a. there has been no continuous passage for temperate species, but the passage served as a filter or even the SW. Arabian and E. African mountains were reached by chance colonization;

b. many species which actually reached SW. Arabia/E. Africa, died out during hotter and possibly drier times;

c. many species were in principle well able to make the traverse, but their foodplants failed to do so or at least to establish themselves permanently in SW. Arabia/E. Africa;

d. many species could not compete with Ethiopian species already living in the more temperate habitats.

It seems to me that the main cause for the low number of glacial invaders is a combination of the first two (maybe three) mentioned. This combination was apparently still more effective in the C. Saharan mountains, where glacial invaders appear to be absent at present.

It would be interesting to know the foodplants of all Palaearctic species in the Ethiopian Region. For the *Lycaena phlaeas* group *Rumex* species have been recorded as foodplants and the *Issoria hanningtoni* group is said to live on *Viola* species. As both plant genera are presumably Palaearctic intruders it is unlikely that the butterflies living on it experienced much competition on the part of the Ethiopian species. This may explain their relative success in the Ethiopian Region.

Butterflies capable of living under higher temperatures could move southward during humid periods, the last of which occurred only about 5000 years ago. This relatively recent contact is reflected by the fact that they are slightly or not at all differentiated in their present C. Saharan and E. African habitats. They were not especially dependent on the mountainous traverses of the more temperate species, but as according to Moreau (1966) the eastern Sahara has always been drier than the western part, we may also speak here of a western and an eastern traverse, keeping in mind that the western traverse did not only comprise the mountainous regions, while the eastern traverse may also have included the Nile Valley.

Also for these species the western traverse was a dead-end road. Although the southward penetration has left various traces in the C. Saharan mountains, all species which ever reached the Ethiopian Region by this way have become extinct there. It is even questionable whether these species were ever able to establish themselves well in the probably rather saturated W. African savanna fauna. This can, however, not be the only reason for their absence in W. Africa as some of these species could establish themselves firmly in E. Africa. Apparently the mountains of E. Africa offer better opportunities for survival of these species too, than the possibly too hot, low-lying steppe and savanna along the southern edge of

the Sahara in W. Africa. Also the sudden disappearance of the Mediterranean vegetation from W. Africa shortly after the Postglacial Climatic Optimum (see Moreau, 1966) may have played a part in the absence of Mediterranean butterflies in W. Africa or at least there may be a common cause.

Also the Palaearctic species capable of living in steppe and savanna environments number very low in E. Africa and SW. Arabia (about six) and in this case again, the cause for the low number may have to be looked for in a combination of desiccation and disappearance of foodplants, assuming that there have ever been more species penetrating so far to the south.

In sum, a southward movement of Palaearctic butterflies across the Saharo-Arabian desert zone has occurred various times during the Pleistocene, but penetration into the Ethiopian Region has only been successful (i.e. with still living progeny) through the eastern traverse, along either side of the Red Sea. The effectiveness of the Red Sea itself, especially at its southern end, as a barrier will be dealt with in Chapter 5.

The northward traverse

For Ethiopian species the Glacial Periods have probably been too cold for a successful northward expansion and a movement in that direction must generally have been confined to periods which were more humid and possibly also warmer than the present one. The last of such periods, the Postglacial Climatic Optimum, occurred only about 5000 years ago and it is to be expected that species, taking this opportunity, have differentiated in the Palaearctic Region very little or not at all. Indeed, eight of the thirteen species of table 3 are not subspecifically distinct in the Palaearctic Region from their Ethiopian representatives and thus, for these species a northward expansion during the Neolithic comes into consideration. Migratory species (*Catopsilia florella, Danaus chrysippus*) may have reached the Palaearctic still more recently; *C. florella* is known from the Canary Islands only since about ten years.

If the Palaearctic representative is subspecifically distinct from the Ethiopian stock, this does not mean a priori that the isolation is of an older age. It is quite well possible that *Colotis evagore* developed its Palaearctic race, *nouna,* during the last 5000 years. However, for the two other species concerned, viz. *Charaxes jasius* and *Borbo borbonica,* the situation is somewhat different as they occur discontinuously in the same subspecific form in the West as well as in the East Mediterranean. The absence of differentiation in this area suggests that the distribution has been continuous up to a rather recent time or that there has been a rather recent range expansion within the Mediterranean area. If an Ethiopian species succeeded in expanding its range northward throughout most of the Mediterranean, it is improbable that during a subsequent isolation the Mediterranean range would remain continuous, and thus the development of a single Mediterranean subspecies is improbable. As a consequence, *Charaxes jasius* and *Borbo borbonica* probably became isolated (and differentiated) in the Mediterranean before the Neolithic and extended their range in this area during this humid period.

The two Palaearctic *Spialia* species, *sertorius* and *orbifer,* are specifically distinct from their Ethiopian relatives. They are believed to have originated from a common Ethiopian stock, of which the Ethiopian *mafa* and the Oriental *galba* constitute the remainder of the progeny. As the geographic variation of *sertorius* and *orbifer* reflects the influence of at least the Last Glacial and the origin of *sertorius* and *orbifer* themselves is the result of glacial isolations, the northward expansion of the Ethiopian stock must have occurred earlier. *S. sertorius* and *orbifer* are not restricted to the Mediterranean Region, but can also live under much cooler conditions, while *mafa* ascends at least to 2000 m in the East African mountains. Therefore, it is possible that the northward expansion occurred during one of the earlier Glacial Periods, as a result of the lowering of the montane zone.

As for the southward movement, two routes were available for the northward movement, a western and an eastern one, but the Ethiopian species did not need mountains on their way, only hot and not too dry country. Thus one would expect that during the Postglacial Climatic Optimum many Ethiopian species expanded their ranges northward over a broad front, with the exception of the eastern Sahara, where conditions seem to have always been unfavourable. Nevertheless, at present very few Ethiopian species live in the Palaearctic Region. There is another remarkable feature: almost all Ethiopian penetrations into the Palaearctic Region appear recent, mostly not older than about 5000 years. Only the *Spialia* species indicate a penetration in the early Pleistocene.

The mainly recent arrival of the present Ethiopian species in the Palaearctic Region may be due to the fact that former penetrations (before the Last Glacial) were largely obliterated by the dramatic climatic change during the Last Glacial. The relatively low number of Ethiopian species in the Palaearctic Region at present indicates that postglacially the passage to the north was difficult or that only few species managed to survive till the present day.

An indication of a northward movement over a broad front is found in the present butterfly fauna of the western Sahara and the Saharan mountains. The butterflies must have reached the mountains during a more humid period and they now live there largely isolated, being surrounded by large stretches of uninhabitable land. As they are scarcely, if at all, differentiated from tropical species, the isolation must be recent and as for the Ethiopian species in the Palaearctic Region, the Postglacial Climatic Optimum comes into the picture as a favourable period for northward range extension.

In view of the isolation and rather severe conditions the number of tropical butterflies in the Saharan mountains is not unimportant. Table 6 and Fig. 6 give the numbers and percentages of tropical (i.e. originating from the area south of the Sahara) and non-tropical species in various regions in the Sahara and NW. Africa. As is to be expected, the mountains closest to the southern edge of the Sahara (Aïr, Ennedi) contain the largest percentages of tropical species. Remarkable, however, is the steep decline in the percentage of tropical species in Ahaggar and further to the north, the more so as in northern Rio de Oro, further north than Ahaggar and close to the southern fringe of the Palaearctic Region, the situation is quite different and the ratio tropical-nontropical species is about the same as in Tibesti. As there were ample opportunities for northward range extension only

Table 6. Number of tropical and non-tropical species in various regions in the Sahara and NW. Africa.
See also Fig. 6

	tropical	non-tropical	total
Morocco-Algeria, N. of Sahara	9	116	125
NW. Sahara	4	13	17
Ahaggar	4	8	12
Northern Rio de Oro[1])	14	6	20
Tibesti	16	7	23
Aïr	22	2	24
Ennedi	21	1	22

[1]) only Pieridae

about 5000 years ago, a large-scale extinction of tropical species in Ahaggar and further north during a glacial period cannot be the reason for the present low number of tropical species. In Europe, the Postglacial Climatic Optimum was followed by the cool and wet Sub-Atlantic (2500—2000 BP) (Moreau, 1955). It is unknown how far NW. Africa participated in the decrease of temperature (except that according to Moreau, 1966, a sudden deterioration took place at the end of the Neolithic), but it is well imaginable that a slight drop in temperature would force tropical species living at the edge of their range to withdraw, while near the coast the ocean can have had a tempering effect, so that the drop in temperature was less strongly felt and tropical species could maintain themselves more easily. If we only consider the rapid fluctuations in the ranges of e.g. *Papilio machaon* L., *Araschnia levana* L., *Polygonia c-album* L., in Western Europe during the last
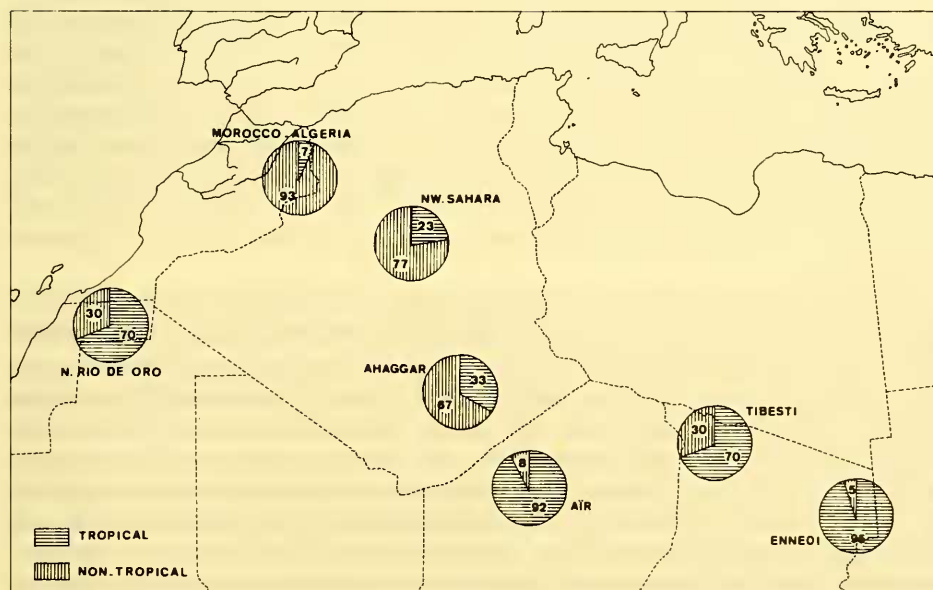

Fig. 6. Composition of butterfly faunas in various regions in northern Africa

century (strongly felt in the Netherlands) which were probably influenced by climatic factors, the above hypothesis is plausible.

Another explanation may be that only few tropical species reached Ahaggar postglacially. According to Moreau (1966) pollen deposits from Tibesti indicate a sudden change in vegetation from Mediterranean to a tropical (Sahelian) one, which was better adapted to drought before the end of the Neolithic. Moreau supposed the Ethiopian plants to have made use of the shores of the expanded Lake Chad (Mega-Chad) that almost reached Tibesti still about 8500 BP, to penetrate as far to the north as Tibesti before the lake was too small and the intervening area too dry. It is understandable that butterfly species following the Sahelian vegetation reached Tibesti (and Aïr?) too late (i.e. it was already too dry) to penetrate still further north.

Thus, the relative poverty of the butterfly fauna of Ahaggar may be due to an extinction of many Palaearctic species, followed by a very limited colonization of Ethiopian species. The fact, however, that only few Ethiopian species live in the Palaearctic part of NW. Africa cannot be entirely due to a limited colonization from the south. The butterfly fauna of northern Rio de Oro shows that the passage through the coastal belt along the Atlantic was easier than across the interior of the Sahara. As this fauna more or less touches the southern fringe of Palaearctic NW. Africa, it appears that the climate of this northern part of Africa is not favourable for Ethiopian species at present, though it may have been in former times. Supposed that a large part of the butterfly fauna of Senegal had ample opportunities to go northwards during the Postglacial Climatic Optimum, the extinction in the north is demonstrated by the following comparison:

In the Niokolo-Koba National Park in SE. Senegal 99 butterfly species have been found (Condamin, 1969) of which 22 are considered relics of a period when the area was better forested, and one (*Vanessa cardui*) is strongly migratory. The remaining 76 species are possible invaders of NW. Africa during the Neolithic. In Morocco, however, only five of these species occur (one tropical species in Morocco is not known from SE. Senegal, viz. *Colotis evagore*). Moreover, in northern Rio de Oro more tropical species of Pieridae have been found than in Niokolo-Koba National Park (14 against 13) and seven of them are not known from the latter area. This suggests a still larger extinction in NW. Africa than indicated by the enormous diverging numbers of tropical butterflies in SE. Senegal and Morocco.

The western route (or rather the area through which passage was possible) was delimited to the east by the waters of Mega-Chad (see above) and the dry eastern Sahara (Libyan desert). In the eastern part of the Saharo-Arabian desert zone the main route to the north will have been the Nile Valley. Braestrup (1947) suggested that even today the middle course of the Nile Valley is too cold to be passed by Ethiopian reptiles and amphibians as the mean and mean minimum temperatures are distinctly lower there than at the Mediterranean coast and in northern Sudan. Apart from drought this may also be a limiting factor to the northward expansion of Ethiopian butterflies today. Thus, since before the Last Glacial only the warm and humid Neolithic is considered for a northward expansion in this area. Also the mountainous routes at either side of the Red Sea have been usable for Ethiopian

species only during this period as at other times they were too dry or too cold or both. Moreau (1966) assumed that during the Neolithic an open to wooded savanna vegetation may have existed in the mountains of SW. Arabia, along the elevated southern edge of the peninsula and in SE. Arabia. Probably a savanna-like vegetation extended northwards following the mountains east of the Red Sea. The route through the mountains west of the Red Sea may have been more difficult to pass as especially in the northern part the mountains are low and vegetation may have been very scarce over long stretches.

Although the eastern traverse (east of the C. Sahara) appears to have been at least as well passable for Ethiopian species as the western one, and the low-lying areas of northern Egypt and the coastal areas of the Middle East must have been favourable for many Ethiopian species to survive, the number of Ethiopian species in the E. Mediterranean equals about that in the W. Mediterranean (the seemingly limited importance of the eastern traverse is biased by the exclusion of Indo-Ethiopian species from this consideration; see paragraph on the indirect West-Palaearctic-Ethiopian affinities, p. 203).

Longstaff (1913, 1916) recorded 95 butterfly species from the White Nile district and southern Kordofan, i.e. from the area fringing the southern edge of the Sahara. The greater part of these species must have been able to go north when the climate improved (became more humid). Nevertheless, only about one quarter of this number (including the species with Indo-Ethiopian distribution) now lives in the E. Mediterranean. Further, Gabriel (1954) listed 97 species of butterflies from SW. Arabia. Excluding the Palaearctic intruders (13), only 20 species (including Indo-Ethiopian ones), i.e. less than one quarter, are also known from the E. Mediterranean.

These facts can lead to one conclusion only: a large extinction of Ethiopian species has taken place in the Middle East during the last 5000 years. It is interesting to note that Moreau (1966) supposed the bird fauna of lower Egypt to have been much richer in species 5000 BP than at present. Apart from proceeding cooling and desiccation, human interference may have played a part in this faunal impoverishment. It appears that Ethiopian species have an extinction rate quite different from Indo-Ethiopian species, see p. 203.

Summary and conclusions. Northward range extension across the Saharo-Arabian desert zone has been possible only during more humid and warmer, or at least not colder, periods than the present one. The last of such periods occurred only about 5000 BP (Postglacial Climatic Optimum). Various traces have been left of a northward movement during this period, but there are indications that the Ethiopian species now living in the Palaearctic are only relics of a much richer Ethiopian fauna that became largely extinct in the Mediterranean only during the last 5000 years by cooling, desiccation and human interference.

Similar northward invasions and subsequent extinctions must have taken place during interrlacial periods, but only a single relic from before the Last Glacial has maintained itself up to the present day, viz. *Spialia sertorius/orbifer*. Evidently
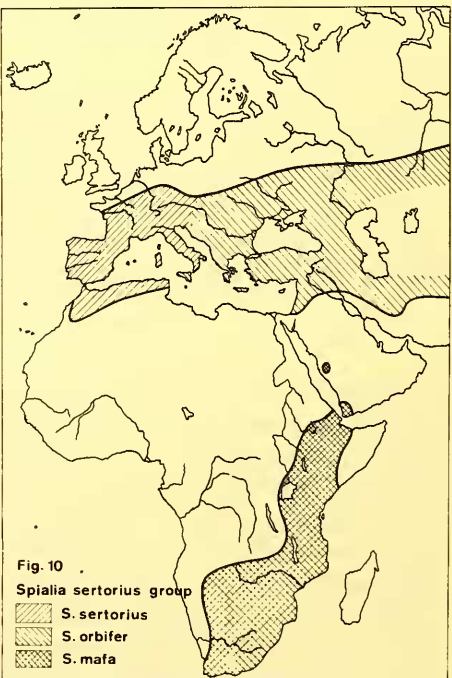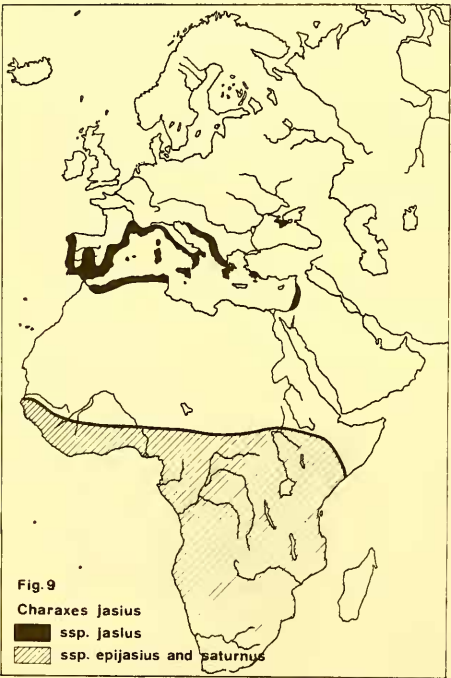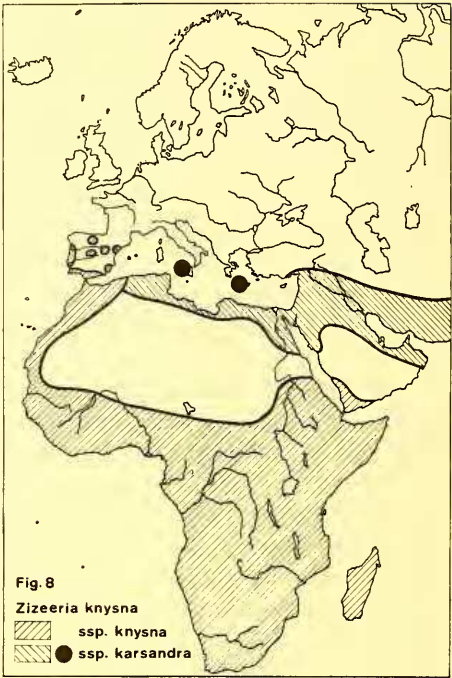
Fig. 7
Colotis evagore
▦ ssp. nouna
▨ various subspecies

Fig. 8
Zizeeria knysna
▨ ssp. knysna
▧ ● ssp. karsandra

Fig. 9
Charaxes jasius
■ ssp. jasius
▨ ssp. epijasius and saturnus

Fig. 10
Spialia sertorius group
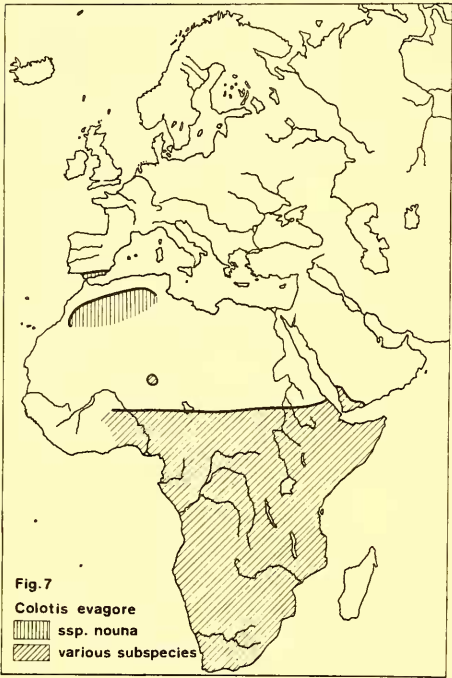▨ S. sertorius
▧ S. orbifer
▦ S. mafa

Fig. 7—10. Butterfly species with Ethiopian ancestry in the Palaearctic Region

the fact that this relic adapted itself to temperate climates has contributed much to its survival.

As for the southward movement, two traverses were possible, separated by the dry Libyan desert. The western route was situated across the entire western Sahara, but most species expanding northwards through the interior of the Sahara could not get further in time, before the desiccation became disastrous, than the Saharan mountains, where they now live as relics. Ahaggar was already too far to the north for many species. The shorter route through the coastal belt along the Atlantic appears to have been open much longer and to have been the main corridor to the north in this part of Africa. The importance of this corridor is indicated by the large number of tropical Pieridae in northern Rio de Oro. In Palaearctic NW. Africa only very few traces are found of the Neolithic connection. The reason is probably twofold: (a) many species could not establish themselves in the mountainous area of NW. Africa, and (b) most tropical species became extinct in NW. Africa during the last 5000 years.

In the east two routes, now impassable for most species, were open during the Neolithic, viz. the Nile Valley and the mountainous area east of the Red Sea. Their relative importance will be dealt with in Chapter 5. Comparison of the E. Mediterranean butterfly fauna with that of areas near the southern edge of the Saharo-Arabian desert suggests a high extinction rate of tropical species in the E. Mediterranean during the last 5000 years.

For Ethiopian species the eastern and western traverses were almost equally important as far as can be judged from the large numbers of species which possibly used these routes and the small numbers still alive in the W. and E. Mediterranean. As, however, Indo-Ethiopian species also used the eastern traverse, it was much "busier" than the western one.

The indirect West Palaearctic - Ethiopian affinities

The Indo-Ethiopian species

The affinities between the Indian and Ethiopian faunas fall outside the scope of this paper, but some of the species common to both regions also occur in the Palaearctic Region and for that reason they come into the scope of the present study. Moreover, they give supplementary evidence of the importance of the eastern traverse (the western traverse does not come, of course, into consideration).

As for the Ethiopian species, only warm and humid periods can have made possible the faunal contact between the Indian and Ethiopian Regions. We are mainly interested in the last of such periods, the Postglacial Climatic Optimum during the Neolithic, as only common species are involved here and as a consequence of the devastating effect of the Last Glacial it seems improbable that an earlier contact (before the Last Glacial) would be still traceable in the Palaearctic Region.

In our treatment of the northward movement through the eastern traverse by Ethiopian species we already mentioned a difference in the (supposed) extinction

rate between Ethiopian and Indo-Ethiopian species in the E. Mediterranean. This difference is, indeed, remarkable. Of the 74 Ethiopian species recorded by Longstaff (1913, 1916) from the White Nile district and Kordofan, which are possible invaders in the Palaearctic Region, only three (i.e. 4%) occur in the E. Mediterranean, but of the 18 Indo-Ethiopian species ten (56%) have been found in the E. Mediterranean. Similar figures are found by analysing the SW. Arabian butterfly fauna (cf. Gabriel, 1954). Of the 65 Ethiopian species and possible invaders in the Palaearctic Region, only four (6%) are known from the E. Mediterranean, but of the 18 Indo-Ethiopian species 13 (72%) occur in that area.

These obvious differences may have two reasons, viz. (a) real different extinction rate, and (b) different use of the eastern corridor. These two reasons are closely related and probably both played a part. If the Indo-Ethiopian species had a better chance to survive, it would mean that they were better adapted to a dry climate or were more eclectic, capable of living in more diverse habitats, than purely Ethiopian species. This would, at the same time, imply that the eastern corridor was longer passable for Indo-Ethiopian species. Their ability of living in diverse habitats is illustrated by the fact that many Indo-Ethiopian species are migratory (cf. Table 4). It may be more realistic to state that the most adaptable species had the best chance for getting an Indo-Ethiopian range, as undoubtedly their adaptability has contributed to the large extent of their range.

In the Palaearctic, the Indo-Ethiopian species are mainly found in the E. Mediterranean, though in Africa they usually occur as far west as W. Africa. As most of the Indo-Ethiopian species, which are lacking in the W. Mediterranean, do occur in the C. Saharan mountains or even northern Rio de Oro (e.g. *Colotis phisadia, Anaphaeis aurota, Catopsilia florella*), it appears that their absence from the W. Mediterranean is due to extinction (see paragraph on the northward traverse, p. 197).

The eremic species

It is impossible to draw a sharp dividing-line between the eremic and Indo-Ethiopian species. To obtain at least a slight idea of the group we may consider the species of Table 4, minus those which are also distributed in Africa south of the equator.

Of some eremic species we can be fairly certain about their geographic origin, e.g. *Pontia glauconome* and *Gegenes nostrodamus*. Such species have been incorporated in the appropriate tables and not in Table 4. The geographic origin of other eremic species is quite uncertain, they have lived so long in the eremic zone that their relationship has become obscure. The Lycaenid genus *Apharitis* is an example of a totally eremic genus. Such species and genera do not belong to the Palaearctic or the Ethiopian fauna and this being so, they are not interesting for the present study. They are the best indication that the barrier between the Palaearctic and Ethiopian Regions is a biome and not a line.

Apart from that it is obvious that their geographic history is closely connected to the alternation of dry and wet periods, and for that reason their distribution and possible geographic variation may indicate possible corridors for faunal exchange

across the eremic zone. However, the number of eremic butterflies is too small for this purpose.

Remaining genera

As said above (Chapter 3, p. 185) the history of the genera *Papilio, Neptis, Vanessa, Libythea* and *Cyclyrius* is obscure, so far Euro-Ethiopian affinities are concerned. This does not mean a priori that these genera did not make use of the Pleistocene corridors, but in view of the rather remote relationship between the European and Ethiopian members of these genera, a recent traverse is very improbable. Moreover, the European members of the genera (with the exception of the anomalous *Cyclyrius*) also occur in East Asia and it is not impossible that most of them have an East Asiatic origin and invaded the West Palaearctic in rather recent times.

An indication of a Pleistocene Indo-Ethiopian contact is found in the Ethiopian *Papilio demodocus,* which also occurs in SW. Arabia, while the closely related Oriental *P. demoleus* extends from E. Arabia eastward. In the other genera such a recent contact is not demonstrable (with the possible exception of the migratory *Vanessa cardui*).

5. BARRIERS OUTSIDE THE DESERT ZONE

The Saharo-Arabian desert zone separates the Palaearctic and Ethiopian Regions, but there are more barriers to a north-south exchange, viz. the Mediterranean and the Red Sea, as Africa today is only connected to other continents by the narrow isthmus of Suez. As this appears to have been also the sole land connection during the whole of the Pleistocene, and it is improbable that all exchange took place across this connection, the effectiveness of the water gaps of the West Mediterranean and the southern Red Sea as a barrier is examined in this chapter.

The West Mediterranean

As said above (Chapter 4, p. 186) various land connections are thought to have existed during the Tertiary across the West Mediterranean. Thus, at some time before the Pleistocene, the butterfly faunas of NW. Africa and the northern part of the West Mediterranean area must have borne a great resemblance. If we suppose that the present gap of water forms an insurmountable barrier for butterflies, the similarity of the butterfly faunas north and south of the gap must be based on this Tertiary contact. It is very questionable whether a contact broken since then would still be discernible at the species level (indicated by the presence of the same species north and south of the present gap).

A more recent landbridge appears to have existed during the Pliocene in the Tunisia-Sicily area. Therefore, one would expect that the butterflies of NW. Africa bear a greater resemblance to those of Sicily than to those of Spain. This is evidently not true, on the contrary, NW. Africa has more species in common with

Spain than with Sicily. On the other hand, a somewhat greater part of the Sicilian than of the Spanish species is represented in NW. Africa. The differences are undoubtedly influenced by the fact that Sicily is much smaller and with a more limited variety of habitats than Spain. To compensate for this, also the butterfly faunas of Andalusia (for a comparison with Sicily) and of peninsular Italy (for a comparison with Spain) have been considered, while the species which are restricted in Spain to the Pyrenees and Cantabrian Mountains have been left out of consideration. The results are represented in Table 7 (the data are extracted

Table 7. Number of butterfly species in various areas (diagonally), number of species shared by pairs of areas, and (in italics) a faunal similarity coefficient for pairs of areas (see text)

	NW. Africa	Andalucia	Sicily	Spain	Sicily & penins. Italy
NW. Africa	125	91	64	93	74
Andalusia	0.552	131	79	131	94
Sicily	0.395	0.516	101	94	101
Spain	0.431	—	0.492	184	131
Sicily & penins. Italy	0.368	0.503	—	0.645	150

from Higgins & Riley, 1970, and Gomez Bustillo & Rubio, 1974). A similarity coefficient has been calculated from the formula FS (faunal similarity) = $\frac{(a,b)}{a+b+(a,b)}$, where a and b are the numbers of species restricted to the regions A and B, respectively, and (a,b) is the number of species common to A and B. This formula allows a quick comparison of resemblances between pairs of regions, though it may be less convenient for further statistical processing.

It appears that the resemblance between the NW. African and Andalusian butterfly faunas is noticeably greater than between the NW. African and Sicilian butterfly faunas. Less noticeable, though still obvious, is the difference between the resemblances of the NW. African-Spanish, respectively the NW. African-Italian butterfly faunas. As the areas Andalusia and Sicily, and also Spain and Italy are more or less comparable in variety of habitats, the above figures suggest that the contact between NW. Africa and Spain has been more intensive or of a more recent date than between NW. Africa and Sicily/Italy, or that the latter area has been subjected to a large-scale extinction of butterfly species which also occur in NW. Africa. For the latter possibility there are no indications at all.

In the above considerations, the direction of the interchange between NW. Africa and Europe has not been taken into account. Of the 125 NW. African butterfly species, 83 can with reasonable certainty be considered northern invaders, the remaining 42 species invaded NW. Africa from the south or east, or we cannot be certain about their geographic origin. Of the 83 supposedly northern species, 14 do not occur in Spain or Italy; they are mainly endemic species which are regarded closely related to European species; further, 67 are also known from Spain and 54 from Italy (incl. Sicily). These numbers are almost the same percentages of the total number of butterflies in the respective regions (Spain

36.4%, Italy 36%), and therefore, it would seem unlikely that either of these two regions contributed more (in relation to its own fauna) to the population of NW. Africa. We can, however, analyse the data further. There are 49 species in Spain (excl. Pyrenees and Cantabrian Mountains) which are lacking in peninsular Italy (and Sicily); of these, 15 (30.6%) occur in NW. Africa. On the other hand, 15 species occurring in peninsular Italy and Sicily are absent in Spain, and of these only two (12.5%) (*Hipparchia aristaeus* Bonelli, and *Satyrus ferula* Fabr.; the latter also occurs in the Spanish Pyrenees) are found in NW. Africa. This again points strongly to the assumption that the connection across the Straits of Gibraltar has been of greater importance to the present relationship between the NW. African and European butterfly faunas than the Sicilo-Tunisian corridor.

The number of species which came from NW. Africa is very small. Indeed, only four species can be listed as such, viz. *Colotis evagore, Tarucus theophrastus, Zizeeria knysna* and *Borbo borbonica.* All occur in Spain, but only the second and third are known from Sicily and peninsular Italy. Consequently, also for the northward exchange the Gibraltar corridor appears to have been most important for the present situation. It is interesting to note here that *Z. knysna* evidently used the Gibraltar as well as the Sicilo-Tunisian corridor, as the Moroccan *Z. knysna knysna* occurs in Spain and the Algerian *Z. knysna karsandra* in Sicily.

Further indications of the importance of the Gibraltar corridor are found in the geographic variation. The excessive splitting performed in most butterflies with regard to their subspecies is a serious hindrance to this kind of examination and for that reason I have extracted the figures given below from Higgins & Riley (1970), who have lumped subspecies to a large extent, with some additional information.

Of the 39 species which occur in NW. Africa, Spain, Sicily and peninsular Italy, and of which at least two subspecies are recognized, seven occur with the same subspecies in all these regions, four with a different subspecies in each region, 17 with the same subspecies in Spain and Italy, but distinct in NW. Africa, three with the same subspecies in NW. Africa but distinct in Spain, and eight with the same subspecies in NW. Africa and Spain, but distinct in Italy. An interesting case is found in *Carcharodus alceae,* which shows two genitalic forms, one restricted to NW. Africa and S. Spain-S. Portugal, the other from S. Spain throughout the remainder of the range of the species, including Italy (De Jong, 1974a).

Conclusion. All observations point to a more recent and more intensive contact between NW. Africa and Europe through the Gibraltar corridor than through the Sicilo-Tunisian corridor. As the Sicilo-Tunisian landbridge was the last terrestrial connection in this area and was severed in the Pliocene, it follows that much or most of the contact took place across the water gap of the Straits of Gibraltar and not through a landbridge. The great resemblance, even subspecific, between the NW. African and Spanish butterfly faunas suggests a regular Pleistocene contact. Apparently, the influence of Tertiary landbridges in the Gibraltar or Sicilian area has been largely overwhelmed by later contacts. The fact that only a rather arbitrary part of the European butterfly fauna succeeded in colonizing NW. Africa

is undoubtedly the result of the filtering effect of the Gibraltar water gap. The Sicilian corridor was apparently much more difficult to pass in the Pleistocene and few species have crossed this large sea gap.

In sum, at least in its western part the Mediterranean has not acted as an insurmountable barrier for north-south exchange, and consequently, its influence on the faunal exchange between the Palaearctic and Ethiopian Regions has been small.

The southern Red Sea

The area between the Red Sea and the Nile is much less elevated than the area east of the Red Sea (see Fig. 1). West of the Red Sea, between northern Egypt and Eritrea, elevations over 1000 m are only found on a series of isolated mountains close to the Red Sea, but east of the Red Sea elevations over 1000 m occur continuously from the Middle East to Yemen. Therefore, the latter area appears to have been most convenient for temperate Palaearctic species to go south. However, such species ran up against the water gap of the Red Sea in their southward expansion, as the Red Sea opened before the Pleistocene. According to Moreau (1966) the width of the Red Sea would have been little affected by the lowering of the ocean level during the glaciations, but as the maximum lowering of the ocean level amounted to at least 100 and probably 200 m, the width of the southern part of the Red Sea must have been influenced largely and a lowering of 200 m must have connected Eritrea to SW. Arabia.

Apart from the Red Sea the temperate Palaearctic species had to cross low-lying grounds to reach the Ethiopian mountains. There is no reason to suppose that at any time during the Pleistocene the habitats of these species were distributed continuously from the Middle East to East Africa. It is, therefore, not surprising that but few temperate Palaearctic species succeeded in colonizing the African mountains. But the present question concerns the effectiveness of the southern Red Sea as a barrier. For some species (cf. Table 2) the Red Sea has been insurmountable, indeed: for the *Hipparchia* stock which gave rise to *H. tewfiki,* and for *Tarucus balkanicus* and *Carcharodus alceae,* the route east of the Red Sea has apparently been a dead-end road, as they did not reach Ethiopia. Other species clearly show that the jump from SW. Arabia to the mountains of Ethiopia has been possible, as they (or one of their subspecies) are (mainly) restricted to SW. Arabia and Ethiopia. They are: *Melitaea abyssinica,* the vicariant species *Lasiommata maderakal* and *felix,* the vicariant subspecies *Lycaena phlaeas pseudophlaeas* and *phlaeas shima,* and *Spialia doris doris.* For the other species of Table 2 a contact across the Red Sea is not needed to explain their present distribution, as they may have gone southward by a route west or west as well as east of the Red Sea. In some cases, especially *Pieris brassicoides, Pontia helice* and the *Issoria hanningtoni* group, it is also feasible that they migrated south through the Arabian mountains, traversed the Red Sea, penetrated the East African mountains and became extinct in SW. Arabia. Other species, less dependent on the cooler climate of the mountains, may have gone southward west of the Red Sea or even through the Nile Valley. I agree with Larsen (in litt.) that the present occurrence of *Gegenes*

nostrodamus along the Nile southward is of a recent date and has to do with the preference of the species for oasis environments. Similar instances may be found in other species as well.

In sum, for Palaearctic species the southern end of the Red Sea has acted as a filter which was probably passed by the majority of the species. This filter has been important for the north-south exchange, as probably most Palaearctic species to go south used the route east of the Red Sea.

For the Ethiopian species which expanded their ranges to the north, the Red Sea did not form a barrier as they could use the route west of the Red Sea and the Nile Valley. Nevertheless, many species crossed the Red Sea and it possibly was the main route for Indo-Ethiopian species. Gabriel (1954) listed 97 Rhopalocera from SW. Arabia, of which 86 are also known from Ethiopia and/or Somalia. If we extract the eight Palaearctic species, 78 tropical species once must have crossed the Red Sea. This number appears large if compared with the about 420 species of Rhopalocera known from Ethiopia (Carpenter, 1935; Gabriel, 1949), but if we consider that Ethiopia is very much larger and has a much greater variety of habitats, it is clear that the crossing of the Red Sea has not given much difficulties for many tropical species. It is unknown whether they could make use of a possible glaciâ land connection or had to jump the water gap during warmer times. At any rate, the crossings have been possible to a recent date, as only 12 of the tropical species in SW. Arabia occur in a subspecific form distinct from the form in Ethiopia. The Tertiary contact before the Red Sea opened at its southern end is not traceable in the present butterfly fauna of SW. Arabia, i.e., such contacts have been swept away by later invasions.

Conclusion. During the Pleistocene the southern end of the Red Sea has been a filter for exchange between Arabia and Ethiopia, but it did not act as a strong barrier, as probably more species passed through than were stopped. The filter effect was performed by the water gap of the Red Sea and for part of the species by the low-lying area between the Red Sea and the Ethiopian highland. During maximum glaciation a landbridge may have existed between SW. Arabia and Ethiopia, but the assumption of such a landbridge is not essential for the explanation of the present distributions.

6.   SUMMARY AND CONCLUSIONS

1. The Saharo-Arabian desert zone has not always hampered the faunal exchange between the West Palaearctic and Ethiopian Regions to the same extent as today. To the contrary, movements across this zone have not been very rare, though survival in the newly won area up to the present day is a rare event.

2. Affinity between the West Palaearctic and Ethiopian Regions at the genus level, without common species or superspecies, may date back to Tertiary times, but does not necessarily do so. In these cases it is often difficult to decide whether the affinity is a result of direct exchange or that one of the regions received the congeneric species from some source outside the other region.

3. The occurrence of a species or superspecies north as well as south of the desert zone is supposed to be the result of a Pleistocene contact across this zone.

4. During the last phase of the Last Glacial Period (Kenya Glacial = last maximum of Würm Glacial), only 12,500-25,000 BP, the temperature decreased to 6°C lower than today in East Africa. This rendered the montane zone in East Africa, the lower limit of which is at 1500 m at present, the possibility to descend to 500 m. Such a lowering of the montane zone facilitated the traverse across the Saharo-Arabian desert zone through mountain ranges by temperate species. Similar conditions must have occurred during earlier Glacial Periods. These periods were not necessarily more humid than the present one and, apart from this, they were generally too cold for Ethiopian species to extend their ranges northward.

More humid periods also occurred more than once during the Pleistocene, the last one during the Neolithic (Postglacial Climatic Optimum), only 4500-7500 BP. During the Neolithic the temperature was about 2°C higher than today. These conditions were favourable for Ethiopian species to go north, but bad for temperate species to go south as their habitats in the mountains became much more isolated and the lowland was too hot. Only Mediterranean species may have been able to move southward. The Ethiopian species were not dependent on mountain ranges, as at least in the western Sahara the warm lowland was also clothed with Mediterranean vegetation. The eastern Sahara appears to have always been dry. The present bare condition of the western Sahara is young and does not date back further than 4500 BP, but similar dry conditions have existed earlier in the Pleistocene.

5. As the Palaearctic species were largely dependent on mountainous areas for their southward expansion, two routes were available, viz. at either side of the Red Sea and from the Atlas Mountains across t e mountains in the Central Sahara. The latter (western) route was a dead-end road as it did not lead to a mountain area in the Ethiopian Region, where the Palaearctic species could survive warmer periods. There are no traces left of a southward expansion through the western route during glacial periods. The occurrence of Palaearctic species in the Central Saharan mountains is supposed to be of a more recent, Neolithic age. The limited importance of the western route was not caused by the Straits of Gibraltar acting as a barrier to the supply of Palaearctic species to the south, as this sea gap was regularly crossed.

The eastern route offered better facilities for Palaearctic species as it led to the mountains of East Africa with ample opportunities for survival during warmer periods. All extant temperate Palaearctic species in the Ethiopian Region used this route, especially through the mountains east of the Red Sea. The southern end of the Red Sea has not acted as an effective barrier on this way. The various degrees of differentiation of the penetrating populations from their Palaearctic ancestors (development of Ethiopian subspecies, species, species groups) indicate a repeated use of the eastern route during the Pleistocene, and the highest degree of differentiation (the *Issoria hanningtoni* group) may be the result of a Late Tertiary invasion.

Mediterranean species (e.g. *Pontia daplidice, Euchloe belemia, Tarucus balkani-*

cus) may have used the Nile Valley and probably also the mountain ranges at either side of the Red Sea to go southward various times during the Pleistocene and for the last time as late as 5000 BP (Neolithic). Probably because their habitat preference largely overlaps that of many Ethiopian species, they never attained an extensive Ethiopian range, while some of the more temperate species eventually reached South Africa and Cameroon. The only exception may be *Gegenes pumilio.*

In view of the opportunities offered and the species available (more than 400 in the West Palaearctic), the number of about 17 successful southward crossings is low. This little success is due to extinction following an initially successful penetration as a result of climatic change (increasing temperature), and perhaps to unknown obstacles on the way, so that not many Palaearctic species ever reached the Ethiopian Region.

6. For the Ethiopian species the Glacial Periods of the Pleistocene were too cold for a penetration into the Palaearctic Region. They only needed a more humid period than the present. The last of such periods, the Neolithic, occurred only about 5000 BP. During the Neolithic a large-scale northward movement through the western Sahara (especially through the coastal regions, but also far inland), the Nile Valley, and probably along the Red Sea took place. Most of the species involved in this movement died out subsequently in the Palaearctic as a result of decreasing temperature, desiccation and human interference. Most relics of the northward penetration are found near the Atlantic coast (northern Rio de Oro), and in the high mountains of the Central Sahara, but Ahaggar was probably too far for most Ethiopian species to be reached before the desiccation became disastrous. Because the isolation of the relics is so young, they are scarcely, if at all, differentiated from their parental Ethiopian stock.

If we suppose that during the Neolithic all possible invaders into the Palaearctic (judged from their present occurrence in the northernmost part of the Ethiopian Region) virtually reached the Palaearctic, we have to consider an extinction rate of Ethiopian species in NW. Africa as well as in the E. Mediterranean, of about 90 % during the last 5000 years.

Humid periods have occurred various times during the Pleistocene, but the resulting northward expansions of Ethiopian species have scarcely left traces, as almost all pre- and interglacial colonizations in the Palaearctic have been swept away by the devastating effect of the glaciations. A notable exception is the common ancestor of the now entirely Palaearctic species *Spialia sertorius* and *orbifer*, which invaded the Mediterranean probably in early Pleistocene times, while two other species (*Charaxes jasius* and *Borbo borbonica*) appear to have gone through at least the last phase of the Würm glacial in the Mediterranean.

The Nile Valley may have been the highway in the eastern part of the Saharo-Arabian desert zone for Ethiopian species bound for the north, but also east of the Red Sea the passage was viable. The gap of the southern end of the Red Sea did not act as an important obstacle on this way.

7. In relation to the total number of butterfly species in the West Palaearctic (more than 400) and Ethiopian (almost 2700) Regions the numbers of successful invasions (i.e. those maintaining themselves up to the present day) (about 17 and

12, respectively) into the other region are small and remarkably different. The difference is due to the fact that the Ethiopian Region offered much more opportunities for survival of Palaearctic species in mountain areas during warmer periods, than the Palaearctic Region for survival of Ethiopian species in lowland areas during colder periods. This also explains why the southward traverses seem to cover a longer period than the northward ones: the species concerned had a better chance to survive.

8. Ecologically more flexible tropical species could attain an Indo-Ethiopian distribution. Several of these species also occur in the West Palaearctic Region. Although it is at present not clear whether the Palaearctic representatives originated from the east or from the south, some may indeed have an Ethiopian origin. Even if we consider all Indo-Ethiopian species in the Palaearctic to be of Ethiopian origin, increasing the number of successful northward crossings to about 20, the relative number of successful crossings is only slightly influenced and the difference with the relative number of successful northward crossings is almost untouched: the difference would only disappear if we could demonstrate more than 100 successful northward crossings.

9. From all considerations above we arrive at the final conclusion:

At present the Saharo-Arabian desert zone separates the Palaearctic and Ethiopian Regions and as a result of the bare condition of this zone faunal exchange is impossible. The desert zone is, however, not the only factor that keeps the Palaearctic and Ethiopian faunas separate. During the last 2 millions of years (the Pleistocene) the desert zone has often been passable in both directions, leading to important faunal exchange, but most penetrating species became extinct as a result of climatic changes. Thus, the Saharo-Arabian region dosed the faunal exchange, and the extinction of colonists subsequently reduced the initial success of the exchange. As both the dosing and the extinction are due to climatic changes and a single climatic change could lead to extensive faunal exchange, we can finally state that the main factor keeping the Palaearctic and Ethiopian faunas apart, at least during the Pleistocene, is the repeated climatic change.

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